

New Investigations into the Late Pleistocene and Early Holocene Rainforest Prehistory of Sri Lanka

Dissertation

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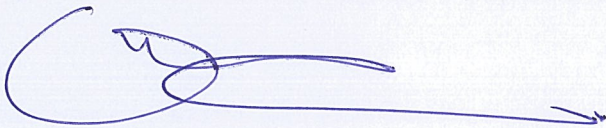
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Declaration of Authorship

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Table of Contents

Introduction	1
<i>Late Pleistocene occupation of extreme environments</i>	6
<i>Late Pleistocene tropical forest occupation in the Old World and its material culture</i>	9
<i>Sri Lanka: A brief geological, geographic, climatic, and environmental introduction</i>	13
<i>Pleistocene archaeological and palaeoecological research in Sri Lanka</i>	14
<i>Remaining questions</i>	17
<i>Research outline and hypotheses for this thesis</i>	20
 Manuscript A	
Specialized rainforest hunting by Homo sapiens ~45,000 years ago	24
 Manuscript B	
Microoliths in the South Asian rainforest ~45-4 ka: New insights from Fa-Hien Lena Cave, Sri Lanka.....	32
 Manuscript C	
Late Pleistocene to Early-Holocene Rainforest Foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena	68
 Discussion	120
<i>Chronology</i>	121
<i>Settlement and subsistence</i>	123
<i>Technology</i>	127
<i>Microolith Technologies</i>	127
<i>Osseous Technology</i>	131
<i>Social and Symbolic Technologies</i>	132
<i>Conclusion and Outlook</i>	134
 References for Introduction and Discussion/Conclusion	138
 Appendices	152
Further notes on stratigraphic phasing of Fa Hien Lena.....	153
Further detail relating to analyses of faunal remains from Fa Hien Lena	163
Lithic Materials from Fa Hien Lena	216
Supplementary References.....	223
 Summary	225
Zusammenfassung (Summary in German)	229
Curriculum Vitae	233
Statement of honour	238

Introduction

The timing, routes, and nature of the dispersal of our species, anatomically modern¹ *Homo sapiens*, Out of Africa during the Late Pleistocene (125-12 ka) remains one of the most debated topics in current palaeoanthropology and archaeology. In terms of timing, there has been a long-running debate between scholars that argue that our species left Africa prior to the end of Marine Isotope Stage 5 (130-80 ka) (e.g. Petraglia et al., 2010; Groucutt et al., 2015, 2017; Hershkovitz et al., 2015; Liu et al., 2010) and those that believe this only occurred c. 60 ka (e.g. Mellars, 2005, 2006; Soares et al., 2011 Mellars et al., 2013). With respect to routes, previous arguments have suggested that our species made use of corridors of grassland that extended across temperate, arid, and tropical environments in Eurasia under climatically favourable conditions (Bird et al., 2005; Boivin et al., 2013). In the context of a ‘southern’ route of dispersal from Africa, through South Asia, and into Southeast Asia and Australasia, alternative narratives have centred on coastal resources as providing a rich source of protein and driving rapid human dispersal around the Indian Ocean rim (Mellars, 2005; 2006). Nevertheless, recent archaeological research across Southeast Asia, Sahul, the Middle East, and notably South Asia, have highlighted potential colonization of a diversity of extreme environments, including deserts, high-altitude settings, and tropical rainforests, during the Late Pleistocene (Deraniyagala, 1992; Summerhayes et al., 2010; Blinkhorn et al., 2013; Roberts et al., 2015a, 2017; Roberts and Stewart, 2018; Zhang et al., 2018).

Over the course of the last decade, it has become increasingly apparent that *H. sapiens* did manage ‘early’ migrations beyond Africa. Not only have new fossils from Jebel Irhoud, Morocco

¹ Note, throughout this thesis, ‘*Homo sapiens*’ and ‘humans’ are used to refer solely to anatomically modern humans, defined on the basis of Stringer (2016), and not to Neanderthals (*Homo neanderthalensis*) or Denisovans.

demonstrated that our species emerged gradually in various parts of Africa from as early as 300 ka (Hublin et al., 2018), but fossil findings in Israel from Misliya Cave indicate that it had made it beyond the African continent by 194-177 ka (Hershkovitz et al., 2018). Early finds of *H. sapiens* fossils at Skhul (120-90 ka) and Qafzeh (100-90 ka) from the same country further confirm an earlier route (Valladas et al., 1987; Stringer et al., 1989; Grün and Stringer, 2000). Although the populations that produced these fossils have often been argued to be part of a failed dispersal event (Shea and Bar-Yosef, 2005), fossil finds of *H. sapiens* in Saudi Arabia *c.* 80 ka (Groucutt et al., 2018), and China *c.* 139-111 ka at Tongtianyan Cave (Shen et al., 2002), 106 ka at Zhirendong (Liu et al., 2010), and *c.* 100 ka at Fuyan Cave (Liu et al., 2015), while hotly contested in the case of some of the Chinese examples (Michel et al., 2016) suggest a wider phenomenon (Bae et al., 2017). Nevertheless, more sustained fossil, material culture, and genetic evidence for our species seems to appear between 60-40 ka in Europe, Asia, and Australia (Conard, 2010; Rabett, 2012; Soares et al., 2011; Pagani et al., 2015; Groucutt et al., 2015; Bae et al., 2017), implying later potential population replacements as the result of renewed migrations from Africa.

The last decade has also produced a diversity of multidisciplinary archaeological records, particularly from sites across Asia, that have enabled more detailed insights into Late Pleistocene human adaptations to environments previously considered to have been intentionally avoided by foragers until much later (Gamble, 1993). One of these, tropical forests, was traditionally assumed to be a barrier to human occupation due to a lack of large protein-rich resource packages, highly-spaced carbohydrates, dense vegetation, and issues of thermoregulation (Bailey et al., 1989; Gamble, 1993; Boivin et al., 2013). Moreover, highly acidic, hydrologically active deposition conditions have been assumed to be poor places to look for well-preserved

archaeological sequences with organic materials that could be used to reconstruct human subsistence (Tappen, 1994). However, archaeological and palaeoanthropological work across Southeast Asia (Barker et al., 2007; Barker and Farr, 2016; Westaway et al., 2017; Roberts, 2019), Melanesia (Gosden, 2010; Summerhayes et al., 2010, 2016), and China (Liu et al., 2010; Liu et al., 2015) has presented growing evidence for the sophisticated use of tropical forest resources from as early as 45 ka, and potentially 100-75 ka (Roberts and Petraglia, 2015). South Asia, and notably the island of Sri Lanka, has also played an increasingly significant role in discussions of the capacity of Late Pleistocene members of our species to inhabit tropical forests. As early as 1992, Siran Deraniyagala argued for the significance of Sri Lanka as part of the story of Late Pleistocene human dispersals by arguing that microlithic technologies, similar to those associated with sophisticated hunting strategies of diverse prey species in ‘Mesolithic’ Europe, dated to older on the island than anywhere else (1992; Perera, 2010). More recently dated to *c.* 38-36,000 years old (Roberts et al., 2015b) they are now far from the oldest globally, but they are the most ancient in South Asia and, at the sites of Fa Hien-lena, Batadomba-lena, and Kitulgala Beli-lena (Figure 1), are found alongside the earliest human fossils and earliest bone tool technologies found in this part of the world. Perhaps most importantly, all of these appear to occur in association with the evergreen lowland tropical rainforest in the southwest of the island (Deraniyagala, 1992; Perera et al., 2011; Roberts and Petraglia, 2015), in contrast to previous suggestions that the first human arrivals in Sri Lanka relied upon a ‘coastal’ route (Mellars, 2006). Faunal evidence indicates a predominance of small tropical rainforest mammals in Late Pleistocene Sri Lankan archaeological sequences, alongside botanical evidence for tropical rainforest trees such as *Canarium* sp. (Deraniyagala, 1992; Perera et al., 2011). The importance of tropical rainforest resources to early humans on the island has also been definitively

demonstrated by the application of stable carbon and oxygen isotope analysis to human and animal tooth enamel found at these sites (Roberts et al., 2015a, 2017).

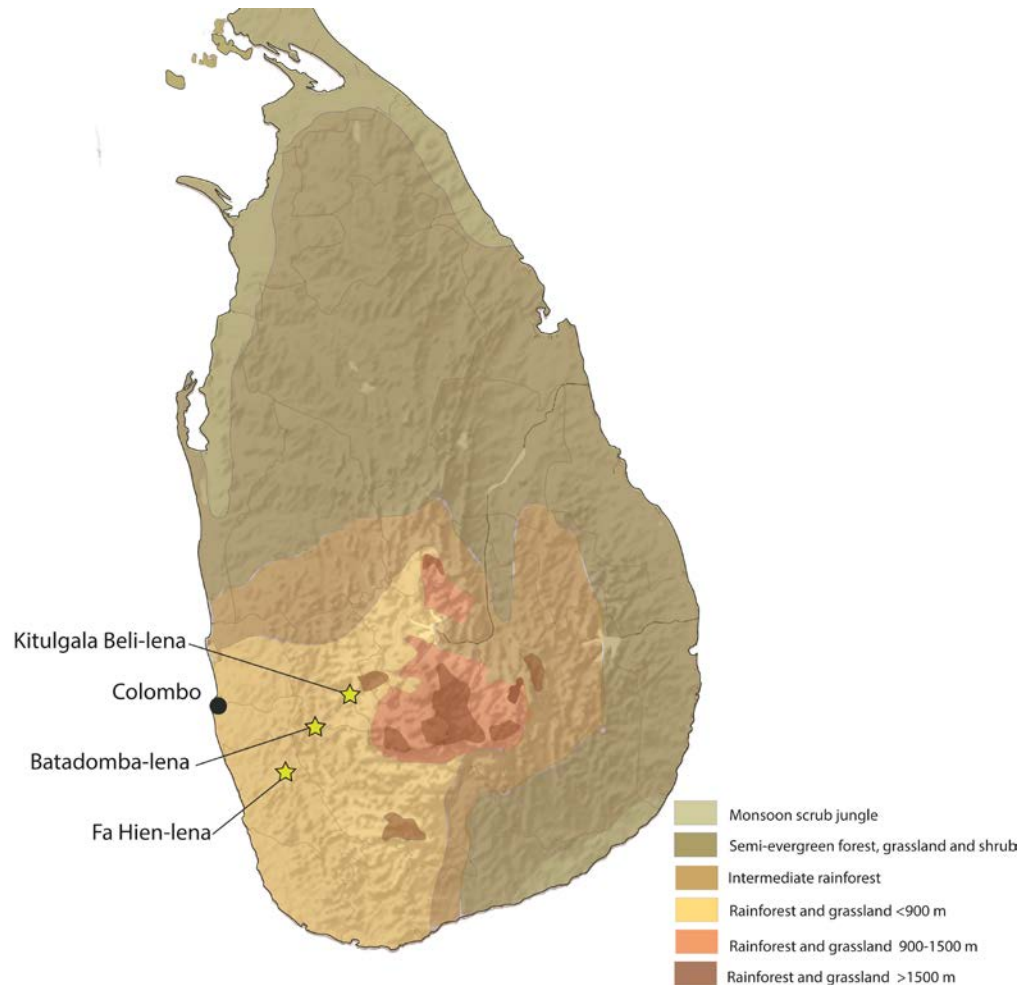


Figure 1. Location of Late Pleistocene sites in Sri Lanka and the island's vegetation zones (after Ashton and Gunatilleke, 1987; Erdelen, 1988).

While Sri Lanka's importance has continued to rise in the context of archaeological and palaeoanthropological discussions of Late Pleistocene human dispersals, research is still in its infancy in this part of the world in this regard. Firstly, with the exception of the site of Batadomba-lena (Perera, 2010; Perera et al., 2011), multidisciplinary excavation of Sri Lankan rainforest sites has been limited, with the apparently oldest site of Fa Hien-lena, home to the

oldest human fossils in South Asia, and the site of Kitulgala Beli-lena notably untouched in this regard (Deraniyagala, 1992; Wijeyapala, 1997; Roberts et al., 2015). Furthermore, both of these sites were dated in the 1980s, prior to the recent development in Accelerator Mass Spectrometry dating, the selection of appropriate, short-lived materials, and novel pretreatment approaches suitable for tropical environments (see Higham et al., 2009). Secondly, there has been little detailed taphonomic and taxonomic analysis of the tropical rainforest fauna at all of the rainforest sites meaning that while we know that humans relied upon tropical rainforest resources, there has been limited detailed insight into what these resources were and what they involved in terms of adaptations. This brings me onto the final key point, the fact that, with two exceptions (Lewis et al., 2014; Perera et al., 2016) there has been no systematic study of the enigmatic microlith and bone tool technologies at Late Pleistocene rainforest sites, and no detailed comparison between the different sequences spanning 38,000 to 3,000 years ago.

In this thesis, I seek to enrich our understanding of Late Pleistocene human adaptations in Sri Lanka, and in Asian tropical forests more generally, by undertaking new multidisciplinary excavation of Fa Hien-lena and Kitulgala Beli-lena. In doing so, I will re-date these sites using the latest radiocarbon and Optically Stimulated Luminescence methodologies available to update the chronology of rainforest occupation in this part of the world. Moreover, I will undertake novel taphonomic and taxonomic analysis of the faunal remains uncovered at the sites of Fa Hien lena and Kitulgala Beli-lena to better understand how humans survived in these challenging environments, and what hunting strategies would have been necessary. Finally, I will follow Lewis et al. (2014) by using multivariate metric analysis of lithic assemblages at these sites to understand the process of microlithic formation, not just within Sri Lanka, but also in comparison to other Late Pleistocene technologies. I will also perform microscopic analysis of

the earliest osseous technologies in South Asia to better reveal their manufacture and use as part of a sophisticated, specialized rainforest subsistence strategy. The application of these methods, and the information they can provide, has the potential to inform wider debates regarding the adaptive flexibility of Late Pleistocene *H. sapiens* as it colonized a diversity of new environments and became the last hominin on Earth.

Late Pleistocene occupation of extreme environments

Roberts and Stewart (2018) recently characterized our species as a unique ‘generalist specialist’, a species that overcomes traditional ecological “dichotomy between ‘generalists’, who can make use of a variety of different resources and inhabit a variety of environmental conditions, and ‘specialists’, who have limited diet and narrow environmental tolerance” (Roberts and Stewart 2018; pp 5). Instead, they argue, *H. sapiens* could not only utilize a diversity of environments as part of broad ecological niche, but *also* simultaneously specialize subsistence *within* these individual environments at the level of local populations. This work in turn follows on from previous researchers, who have highlighted the special capacity of our genus, and notably our species in particular, to deal with climatic and environmental variability (Gamble, 1993, 2013; de Menocal, 2001; Potts, 2002; Potts et al., 2018). Roberts and Stewart (2018), however, draw upon archaeological palaeoanthropological, and palaeoenvironmental data accumulated across Africa, Eurasia, and the Americas over the course of the last decade that demonstrates specialized local adaptations to deserts, high altitude environments, the palaeoarctic, and tropical forests, as well as coastal and grassland environments traditionally favoured by archaeologists in discussions of human behavioural development and migration.

Deserts had, until recently, generally been assumed to be unpromising places to look for evidence of Late Pleistocene human dispersals. However, much publicized work in the Arabian Peninsula demonstrates our species made it to the interior of the Arabian Peninsula during MIS5 (Groucutt and Petraglia, 2012; Groucutt et al., 2018). Middle and Late Palaeolithic assemblages have also been argued to represent the occupation of the Thar Desert of India at various points in the Late Pleistocene (Blinkhorn et al., 2013). The discovery of Aterian Middle Stone Age (MSA) stone tools across the Sahara Desert from as early as 145 ka, similarly demonstrate the occupation of present-day deserts by Pleistocene hominins (Richter et al., 2010; Scerri, 2017). While Aterian lithics in the Sahara have been argued to be deposited by populations specialized in surviving aridity (Garcea et al., 2012), in all of the above cases desert colonization seems to have occurred alongside the presence of palaeolakes and extensive drainage basins, (Armitage et al., 2011 Drake and Breeze, 2016; Groucutt et al., 2018). These areas await the continued application of palaeoenvironmental research in contexts immediately associated with human occupation in order to test, in more detail, the conditions encountered by our species, and perhaps other hominins, during the Late Pleistocene. Interestingly, a recent study of Late Pleistocene occupation of the Kalahari Desert suggests that humans may have occupied sites during phases of limited surface water, implying some kind of adaptation to arid conditions (Robbins et al., 2016).

There has also been growing evidence for Late Pleistocene human occupation of high altitude settings, with sparse, patchy resources, cold temperatures, and even low oxygen in some instances. At sites such as Melikane in the Highland Kingdom of Lesotho human foragers lived in environments higher than 2,000 m a.s.l. from at least 80 ka (Stewart et al., 2012), and at Ntloana Tsoana and Ha Makotoko in the same nation they seemingly persisted through a series

of climatic fluctuations in the Terminal Pleistocene (Roberts et al., 2013). Humans also survived in dry, high-altitude settings *c.* 2,100 m a.s.l. in the Ethiopian Highlands from *c.* 45 ka (Brandt et al., 2012). Until recently, the earliest evidence for high-altitude occupation beyond Africa came *c.* 13 ka in the Andean Plateau of Peru at the remarkable altitude of 4,300 m a.s.l. (Rademaker et al., 2014). However, in this year, archaeological evidence dating from 40,000 to 30,000 years ago demonstrated human occupation at 4,600 m a.s.l. on the Tibetan Plateau (Zhang et al., 2018). While more remains to emerge in relation to the subsistence strategies practiced at these altitudes, and the prevailing environmental conditions, low oxygen conditions, together with likely cold stress and unpredictable weather would have certainly necessitated some form of novel, specialized adaptations.

Another series of cold environments apparently occupied by *H. sapiens* from 45 ka onwards are those of the palaeoarctic. Bones with evidence for butchery indicate that our species, had reached as far north as 72°N at a time of significant cold (Pitulko et al., 2016), though it cannot currently be completely ruled out that these marks were made by Neanderthals or perhaps even Denisovans. The tree-less open landscapes of this cold steppe region with long winters, extensive permafrost, and limited useful plant growth seem to have been overcome by a focus of hunters on mammoth herds that provided food, as well as raw materials for tools, clothing, and also house structures (Nikolskiy and Pitulko, 2013). Recent radiocarbon dates on cut-marked bones from Bluefish Caves, Canada dating to 24 ka suggest that humans may also have adapted to cold, glaciated environments in the Americas at the height of the LGM (Bourgeon et al., 2017). Together, this evidence is suggesting that by at least *c.* 80-50 ka *H. sapiens* expanded to higher-elevation and more arid niches than its hominin predecessors and contemporaries, and by *c.* 45 ka was rapidly colonizing a range of palaeoarctic settings. Nevertheless, in most cases higher-

resolved palaeoenvironmental datasets, directly associated with traces of our species (including fossils and detailed evidence for subsistence), are required to determine the extent to which novel adaptations were required by our species to enter these regions (Roberts and Stewart, 2018). One set of environments where such records have already begun to emerge on a global scale, however, is tropical forests (Roberts, 2019).

Late Pleistocene tropical forest occupation in the Old World and its material culture

Over the past 60 years various scholars have argued that humans occupied the tropical forests of western and Central Africa as early as the Middle and Late Pleistocene (Clark, 1963; Barham, 2001; Mercader, 2002a,b; Taylor, 2011, 2016). In particular, the heavy duty, large bifacial sub-triangular ‘picks’, core-scrapers, and coarse bifaces of the Sangoan (Barham and Smart, 1996; Barham, 2001) and bifacially flaked lanceolate points of the Lupemban (Clark, 1963; Barham, 2001) have been associated with tropical forest distributions of hominins and focused subsistence activities (Cole, 1967, Barham, 2001). The Sangoan, stratigraphically located below the Lupemban at Kalambo Falls, (Barham, 2002), has been reported from within evergreen rainforest at Bete and Guabuo in the Ivory Coast *c.* 254 ka (Lioubine and Guede, 2000; Mercader, 2002a). Palynological analysis of Atlantic coast marine cores has been argued to indicate open and closed forest, respectively, at these two sites during the period of occupation (Mercader, 2002a). Similarly, Lupemban finds within the Ogooué Basin and Mosumu in Equatorial Guinea, *terminus ante quem c.* 30-20,000 cal. years BP, have been associated with tropical forest pollen (Mercader, 2002a). Nevertheless, these ‘off-site’ records are difficult to associated with generally poorly preserved archaeological sequences and there are no direct insights into subsistence strategies (Taylor, 2011, 2016; Roberts and Petraglia, 2015). It is only

after 40 ka that extensive and specialised human settlement and use of Africa's tropical forests emerges (Mercader, 2002a; Roberts and Petraglia, 2015).

Southeast Asia is the possible home of some of the earliest *H. sapiens* fossils in tropical forests. Teeth at Panxian Dadong (c. 300-130 ka) and Fuyan Cave (c. 120-80 ka) in South China are found with fauna indicative of mixed, dry tropical forest (Schepartz et al., 2000; Liu et al., 2013, 2015). While the dating and species identifications of these fossils remains debated (e.g. Michel et al., 2016), other human fossils at Lida Ajer, Sumatra c. 73-63 ka (Westaway et al., 2017) and Tam Pa Ling, Laos c. 60-46 ka (Demeter et al., 2015) have been argued to have tropical rainforest associations. The most detailed evidence for Pleistocene tropical forest use by our subspecies, however, comes from the Niah Caves, Borneo. Here, coarsely flaked stone tools are found in association with some of the earliest bone technology in Southeast Asia, the processing of toxic tropical plants, and a specialised hunting focus on wild boar and some arboreal primates (Barker et al., 2007; Barton et al., 2009; Barker, 2013; Barker and Farr, 2016). Here, and at various Late Pleistocene sites on mainland and Island Southeast Asia, human occupation appears to have focused on mosaic tropical forest and grassland habitats rather than uniform evergreen rainforest (Barker et al., 2007; Rabett, 2012; Roberts and Petraglia, 2015). At some of these sites, notably in South China, Thailand, and Vietnam, these sites are linked to 'core and flake' Hoabinhian technologies (Kipfer, 2000; Bellwood, 2007; Ji et al., 2016). More specialized use of tropical rainforest habitats, and a diversification of lithic and bone tool technologies, occurs from the Terminal Pleistocene in the region (Rabett, 2012).

In Sahul (the landmass that connected New Guinea, much of the rest of Melanesia, and Australia) and the Bismarck Archipelago, Late Pleistocene tropical forest occupation is found in a somewhat different setting. Here, archaeologists have found evidence for human activity,

including stone axes, at sites dating to between 49 and 43 ka at 2,000 m a.s.l. in the Ivane Valley of Papua New Guinea (Summerhayes et al., 2010, 2016). Starch grains of *Dioscorea* yams and charred pandanus nuts indicate the importance of montane tropical rainforest environments to these populations (Summerhayes et al., 2010). In the Ivane Valley, as well as at Late Pleistocene sites in New Ireland, patterns of lithic production (Pavlides, 2004; Summaheryes and Ford, 2014), as well as seasonal cold temperatures at high altitude (Gosden, 2010), suggest that tropical forest foragers were small, highly mobile groups, flexibly exploiting local raw materials as part of seasonal movement between a variety of environments and ecologies (Pavlides, 2004; Leavseley, 2007; Gosden, 2010; Summerhayes and Ford, 2014; Summerhayes et al., 2016; Roberts, 2019). As in Southeast Asia, there is limited evidence for specialized forest subsistence, with mosaic tropical ecologies in New Ireland, New Guinea, and also the Bismarck Archipelago providing the basis for subsistence (Roberts, 2019). Furthermore, more intensive human utilization of tropical forests is seen from *c.* 25 ka and into the Holocene (Pasveer, 2004), including the deliberate transport of small wild mammals between tropical forest settings (Allen et al., 1989; Gosden and Robertson, 1991).

From this brief review, it is clear that Pleistocene members of our species occupied a huge variety of environments that come under the broader heading of ‘tropical forests’. As reviewed elsewhere by Roberts and others (Roberts et al., 2016; Roberts, 2019), the montane tropical rainforest of Highland New Guinea, the peat swamp tropical forests of Borneo, and the evergreen rainforests of these regions and Africa would have represented very different opportunities and challenges for human foragers. This variation only increases when we take into account recently published evidence from Panga ya Saidi, Kenya for the use of tropical coastal forest between 78 and 1 ka (Shipton et al., 2018). Furthermore, the current evidence from Asia highlights that Late

Pleistocene humans pre-20 ka seemingly preferred the seasonal use of a diversity of tropical forest, and in some cases also grassland, habitats (Roberts and Petraglia, 2015). In addition, while there is definitive evidence for tropical forest use in Southeast Asia and Sahul from at least 45 ka (e.g. Barker et al., 2007), and perhaps 70 ka (Westaway et al., 2017), as well as potential evidence for tropical forest occupation in Africa from 100-200 ka (Barham, 2012; Mercader, 2002a), the exploitation of these settings seemingly intensifies in all three of these regions after 20 ka, notably the time at which the tropical forests of Central and South America also begin to be occupied (Piperno, 2011).

This review also highlights that there are remarkably few instances where detailed archaeozoological, archaeobotanical, and, significantly, taphonomic, studies enable systematic investigation of the subsistence strategies practised by human foragers in tropical forest settings in the Middle and Late Pleistocene. Furthermore, in many cases the use of radiocarbon dates with adequate pretreatment techniques (see Higham et al., 2007, 2009) or the limited application of luminescence dating techniques to tropical sequences has led to limited chronological resolution. Finally, there have been few analyses of lithic and organic technologies in the context of their production and use (though see Pavlides, 2004; Langley et al., 2010; Taylor, 2011, 2016; Lewis et al., 2014). There are some exceptions, notably the records from the Niah Caves, Borneo (pre-45 ka) (Barker et al., 2007; Higham et al., 2009) and Panga ya Saidi, Kenya (Shipton et al., 2018), that are yielding highly diverse insights into Pleistocene human foraging activities in the tropics. Nevertheless, these records remain few and far between meaning that effective comparison of adaptations across space and time is challenging. Multidisciplinary excavation and post-excavation analysis in Sri Lanka, at the southern tip of South Asia, across

the past ten years has, however, begun to improve this picture at a key point between tropical Africa and tropical Southeast Asia, Melanesia, and Australia.

Sri Lanka: A brief geological, geographic, climatic, and environmental introduction

The c. 65,610 km² island of Sri Lanka lies just under 50 km beyond the southern tip of the Indian subcontinent. Geologically, 90% of Sri Lanka is made up of metamorphic crystalline rocks, with the remainder consisting of Jurassic, Tertiary, and Quaternary sedimentary rock (Cooray, 1967, 1994). Pre-130 Ma, Sri Lanka linked east and west Gondwana before it and India separated from this super-continent. Today, a very steep geological shelf flanks Sri Lanka to the West, South, and East. Roberts et al. (2015a) use modelling of GEBCO.08 bathymetry, however, to show that the northern edge of Sri Lanka would have been connected to the Indian mainland with decreases of sea-level of just 10 m. This ‘land bridge’ could have been larger than 100 kilometres wide should 50 m changes have occurred. Fossil reef data shows that, indeed, over the course of the Pleistocene Sri Lanka and India were connected (Rohling et al., 1998), including during the peak of the last glacial, before becoming completely isolated in the Early-Middle Holocene following sea level rise after the LGM (Vaz, 2000; Ranasinghe et al., 2013). The island has since been separated throughout the Middle and Late Pleistocene (Roberts et al., 2015a).

Most of Sri Lanka is consists of low-lying plains (30-200 m a.s.l.), however, the island’s ‘central highlands’ reach to greater than 2,500 m a.s.l.. This altitudinal variation results in temperature gradients from an annual average of c. 27°C in the lowlands to 18°C in the highlands (Erdelen, 1988; Roberts et al., 2015a). Nevertheless, as with many tropical regions, it is rainfall that is the dominant climatic factor that structures environments in Sri Lanka. The Indian Ocean Monsoon, and its interaction with the topography of the island, dictates the amount and seasonality of

rainfall over the island (Wang et al., 2005; Gayantha et al., 2017). Between May and October the southwest of Sri Lanka has its ‘wet season’, while the northeast of the island receives most of its precipitation between December and March (Roberts et al., 2015a). These climate patterns allow Sri Lanka to be divided into ‘zones’ based on annual precipitation amounts (Cooray, 1948; Gaussen et al., 1965). S.U. Deraniyagala (1992) has comprehensively translated these ‘zones’ into effective ‘ecozones’ characterized on the basis of prehistoric human carrying capacities and exploitable flora and fauna (Deraniyagala 1992).

Most recently, Roberts et al. (2015a) modelled annual precipitation across Sri Lanka using Worldclim 1.3 records of international precipitation. They found that in descending order, the southwestern ‘Wet Zone’ receives between 4,840 and 2,201 mm of annual rainfall, the ‘Intermediate Zone’ which forms an arc from the western coast to the island’s southern tip receives between 1,701 and 2,200 mm, and the ‘Dry Zone’ receives between 1,001 and 1,700 mm. These climatic divisions are also documented in Sri Lanka’s vegetation. The island’s dense tropical evergreen rainforest is found in the southwestern ‘Wet Zone’, while moist deciduous rainforest and semi-evergreen rainforest cover the ‘Intermediate Zone’ (Ashton and Gunatilleke, 1987; Erdelen, 1988; Gunatilleke et al., 2005). The ‘Dry Zone’ is home to more open, dry-adapted forest, mangrove forest, as well as large expanses of arid-adapted shrubs and grasslands (Erdelen, 1988). In turn, these vegetation structures support different fauna, and Deraniyagala (1992) notes the dominance of medium to large mammals (e.g. sambar deer, elephants) in the more open environments of the ‘Dry Zone’, while ‘Wet’ and ‘Intermediate’ Zone forests consist of smaller, often semi-arboreal and arboreal, mammalian prey such as various monkey species.

Pleistocene archaeological and palaeoecological research in Sri Lanka

There are tentative hints for a ‘Middle Palaeolithic’ period in Sri Lanka. Tools made of quartz and chert of ‘Middle Palaeolithic’ appearance have been found in ancient coastal dunes designated the Iranamadu Formation, for example at the site of Minihagal-kanda (Deraniyagala 1992). These are undated as of yet, however. Tools of the Microlithic tradition, characterized by < 2 cm-long quartz stone tools, secondarily trimmed into predetermined forms such as geometric microliths, have been a primary focus of Pleistocene archaeologists in Sri Lanka (Deraniyagala, 1992; Perera, 2010; Perera et al., 2011; Roberts et al., 2015b; Lewis et al., 2014). Previously termed the ‘Mesolithic’ based on perceived similarity of these toolkits with the developed microlithic toolkits of Terminal Pleistocene Europe (Deraniyagala, 1992), these forms of lithic technology are found in association with the earliest fossil evidence for *H. sapiens* in a series of sites in the ‘Wet Zone’ rainforest of the island (Roberts et al., 2015a).

The earliest confirmed appearance of the Microlithic tradition, and human fossils, is at Fa Hien-lena cave and Batadomba-lena rockshelter, deep within the Sri Lankan Wet Zone. By the 1990s, these had already been dated to 33,000 uncal. years BP and 28,500 uncal. years BP (Deraniyagala, 1992; Wijeyapala, 1997), respectively. Additional dates and re-calibration have since dated the Fa Hien-Lena sequence to between 38-35,000 to 5,000 cal. years BP (Roberts et al., 2015a) and the Batadomba-lena sequence to 36,000 to 12,000 cal. years BP (Perera et al., 2011). An additional Wet Zone cave site of Kitulgala Beli-lena has been dated to between 31,000 and 2,700 cal. years BP (S.U. Deraniyagala, 1992; Roberts et al., 2015a). While all three of these sites have provided evidence for Late Pleistocene human fossils (Kennedy et al., 1987; Deraniyagala, 1992; Kennedy, 2000), yet the enigmatic ‘Microlithic’ technologies associated with this early tropical arrival have only been systematically studied at Batadomba-lena (Lewis et al., 2014). Similarly, while bone tools have been found throughout the Batadomba-lena

sequence, and tentatively documented at Fa Hien-lena, insights into their production and use have remained somewhat superficial (Perera et al., 2016).

In contrast to the other Old World regions noted above then, the earliest human fossils, microlith technologies, and bone technologies are associated with an apparent specialization in lowland evergreen rainforest resource use in Sri Lanka, from first appearance *c.* 38 ka through to 3 ka (Perera et al., 2011; Roberts and Petraglia, 2015; Roberts et al., 2016). Moreover, stable carbon and oxygen isotope data from human and fauna fossils indicate a persistent technological continuum of lithics through periods of climate change in the Late Pleistocene and into the Holocene (Roberts et al., 2017). This pattern of colonization and resilient adaptation would seem to make Sri Lanka a particularly significant instance of rapid, specialized, and sustained Late Pleistocene adaptation to extreme tropical environments. However, a lack of detailed taphonomic study of faunal assemblages, an absence of cross-disciplinary study at Fa Hien-lena and Kitulgala Beli-lena, and out-dated chronologies have left the exact nature of subsistence practices in this part of the world somewhat obscure. Moreover, regional discussions have been inhibited by an undue focus on an isolated Batadomba-lena sequence, limiting the detail possible in discussions of changing patterns through time across the ‘Wet Zone’ rainforests of Sri Lanka more widely.

This is particularly problematic given a lack of detailed ‘off-site’ palaeoenvironmental data in Sri Lanka. Premathilake and Risberg (2003; Premathilake, 2012) have produced a pollen sequence from the Horton Plains in the central Highland Plateau to argue for extensive tropical forest in Wet Zone Sri Lanka prior to fluctuations at the LGM and across the Terminal Pleistocene/Holocene transition. However, to what extent this highland record is relevant to local environments exploited by humans in the lowlands remains debated. There are also currently no

well-resolved marine cores in the vicinity of the island of Sri Lanka, leaving regional discussions of climatic and environmental change, beyond the site of Batadomba-lena, to be largely based on broad-scale global models (e.g. Boivin et al., 2013). The extant data seem to indicate that the Microlithic tradition only spread into ‘Intermediate’ and ‘Dry’ Zone environments from the Terminal Pleistocene at the sites of Balangoda Kuragala and Bellan-bandī Palassa, respectively (Perera, 2010; Roberts et al., 2015b), although investigations in the coastal dune sites of the Iranamadu Formation in the future could prove otherwise. From *c.* 6.5 ka, Microlithic tradition sites extend deep into the Dry Zone at interior sites and a series of coastal shell middens (P.E.P Deraniyagala, 1955, 1956, 1963; Deraniyagala, 1992). Tentative evidence for the transition from the Microlithic tradition to the Iron Age has been suggested at *ca.* 3 ka, though this process remains largely unexplored (Deraniyagala, 1992, 2007).

Remaining questions

Based on the above, I have identified four clear avenues of enquiry that promise to greatly enrich our understanding the prehistoric tropical forest adaptations of foragers in Sri Lanka as well as the capacities of our species more broadly. Firstly, is it possible to enrich our chronological understanding of occupation patterns and human behaviour in the ‘Wet Zone’ of Sri Lanka? Based on current chronological assessment, Fa Hien-lena, at 38 ka, represents the oldest site in the tropical rainforest zone of Sri Lanka; yet these dates are insecure and need to be re-assayed using state-of-the-art dating technology. Furthermore, both Fa Hien-lena and Kitulgala Beli-lena appear, on the basis of current radiocarbon dates, to span the LGM and into the Holocene, whereas Batadomba-lena seemingly records an occupation hiatus at 12 ka following occupation through the LGM (Perera et al., 2011). Thus, the re-excavation and development of higher

chronological resolution at Fa Hien-lena and Kitulgala Beli-lena when combined with the recent research at Batadomba-lena (Perera, 2010; Perera et al., 2011), promises to enable us to track changes in human behaviour and adaptation over important climate transitions in Sri Lanka, and to determine broader settlement patterns

In the context of human behaviour, is it possible to elucidate the use of the enigmatic lithic and bone tools industries of Sri Lanka? In Pleistocene archaeology ‘microlith’ technologies have often been associated with the development projectile technologies and the more efficient hunting of medium to large game mammals in relatively open habitats (Ambrose, 2002 Mellars, 2005; Shea and Sisk, 2010; Shea, 2011). The appearance of quartz artefacts occasionally fashioned into geometric microliths in Sri Lanka is therefore somewhat surprising, especially given that other cases of Late Pleistocene tropical forest occupation in Southeast Asia and Melanesia are associated with more coarsely flaked lithics (Pavlides, 2004; Reynolds, 2013). Similarly, bone tool technologies are rare in other Late Pleistocene tropical settings, perhaps as a result of preservation biases, or, as in the case of Southeast Asia, they appear in great intensity only from the Terminal Pleistocene onwards (Rabett, 2012). Nevertheless, despite the significance of Sri Lanka for placing microlith and bone tool technologies in a wider global context, especially in relation to their environmental associations, there have been few studies focused on their production, form, and uses (Lewis et al., 2014; Perera et al., 2016). Those that have been done have mainly focused on comparisons as part of dispersal hypotheses (Lewis et al., 2014) or have been somewhat superficial (Perera et al., 2016).

When considering questions of the use of these different technologies it is also important to ask, what animals were humans making use of, how did they manage their populations, and how are these remains reflected in the archaeological record? Zooarchaeological and archaeobotanical

research at Batadomba-lena has revealed that monkeys and squirrels made up the majority of the mammalian assemblages, while tropical tree nuts (*Canarium* sp.) were also used (Perera et al., 2011). Nevertheless, a lack of detailed taphonomic research has hindered exact quantification and understanding as to how humans exploited the different prey types available in Sri Lankan palaeoforests. For example, the study of population structures can hope to distinguish between selective hunting and indiscriminate exploitation and, perhaps, trapping. Without detailed taphonomic understanding it is also difficult to compare changing proportions of different prey types through time and between different sites. Finally, an absence of any form of systematic zooarchaeological work at Fa Hien-lena and Kitulgala Beli-lena has made regional patterns of prey exploitation, as well as changing hunting strategies from the Late Pleistocene, through the LGM, and into the Holocene, difficult to discern at any level of detail.

This brings me onto the final question I wish to pose in this thesis: how did human behaviour change with environmental change across the Late Pleistocene and into the Holocene in the ‘Wet Zone’ rainforests of Sri Lanka? Existing palaeoenvironmental data from the Horton Plains indicates that the LGM witnessed a reduction in tropical rainforest extent in the ‘Wet Zone’ (Premathilake and Risberg, 2003). Stable carbon and oxygen isotope analysis of fauna supports this and indicates that the tropical evergreen rainforest of the ‘Wet Zone’ at Batadomba-lena was more open between 36 and 12 ka, than it was at Fa Hien-lena between 12 and 3 ka (Roberts et al., 2015b, 2017). Nevertheless, diverse ‘on-site’ palaeoenvironmental data, in the form of mollusc, archaeobotanical, archaeozoological, geomorphological, and stable isotope analyses, remains lacking beyond Batadomba-lena (though see Kourampas et al., 2009; Roberts et al., 2015b). Expansion of multidisciplinary study of palaeoecologies alongside detailed technological analyses to the sites of Fa Hien-lena and Kitulgala Beli-lena has much to contribute to our

understanding of changes in the habitats and behaviours of human foragers in Sri Lanka across a series of key climatic periods.

Research outline and hypotheses for this thesis

I have put in place the following plan, with corresponding hypotheses, in order to address the above questions. Firstly, I will undertake renewed, multidisciplinary excavation at the sites of Fa Hien-lena and Kitulgala Beli-lena. This includes the re-dating of these sites using radiocarbon dating with pretreatment methods suitable for Late Pleistocene tropical environments (Higham et al., 2009) and, where appropriate, Optically Stimulated Luminescence dating. It also involves the placement of the obtained dates into new Bayesian chronologies for each of these sites, as well as the existing dates from the site of Batadomba-lena (Bronk Ramsey, 2009; as per Shipton et al., 2018). I hypothesize that the application of these methods will extend the occupation of the ‘Wet Zone’ evergreen lowland rainforests of Sri Lanka back in time; as such methods did at the Niah Caves (Higham et al., 2009). This will, in turn, make the human fossils, bone tool technologies, and microliths found at the ‘Wet Zone’ sites of Sri Lanka some of the oldest of their kind in Asia and, indeed, Europe. In addition, I also hypothesize that together the chronologies from Batadomba-lena, Fa Hien-lena, and Kitulgala Beli-lena will document persistent use of the tropical forests of Sri Lanka from the Late Pleistocene, through the LGM, and across the Terminal Pleistocene and Holocene boundary. Renewed chronological understanding would enable more detailed comparison of the Sri Lankan record of tropical forest foraging with that recorded in Southeast Asia and Melanesia.

Secondly, I will perform systematic analysis of lithic technologies and bone tool technologies at Fa Hien-lena and Kitulgala Beli-lena. By undertaking detailed morphometric analysis at these

sites I will compare the production and form of lithics to the one existing study from Batadomba-lena (Lewis et al., 2014). I will also compare the patterns of production to other records from across South Asia and tropical Southeast Asia (Reynolds, 2013). Similarly, systematic analysis of bone tool technologies uncovered from Fa Hien-lena and Kitulgala Beli-lena will provide the first morphometric and chaîne opératoire study of these osseous toolkits in Sri Lanka, enabling their comparison with other records now available from Late Pleistocene Southeast Asia (Langley et al., 2010). I will also attempt preliminary use-wear analysis of the bone tools from Fa Hien-lena and Kitulgala Beli-lena to better understand their use. I hypothesize that the microliths represent a focused pattern of reduction to produce small flake-blades for use as armatures in projectile technologies used in the hunting of tropical forest game. I also hypothesize that the bone tools had similar functions and were perhaps particularly beneficial in the hunting of fast-moving arboreal and semi-arboreal prey. In turn, I hypothesize that these uses explain the variation in the lithic and bone tool records of Sri Lanka relative to those found in the Late Pleistocene in Southeast Asia and Melanesia.

Thirdly, I will undertake the first detailed taphonomic study of zooarchaeological remains uncovered from the ‘Wet Zone’ archaeological sites of Sri Lanka. I will sort, count, measure and, where possible, identify all bone fragments excavated from Fa Hien-lena and Kitulgala Beli-lena using vertebrate comparative collections. All fragments will be studied for natural, animal, and anthropic modifications, including weathering (Behrensmeyer, 1978), abrasión (Shipman and Rose, 1988), burning (Shipman et al., 1984), staining, and butchery marks (Fernandez-Jalvo, Y. & Andrews, 2016). The size of fragments will also be recorded in order to study patterns of fragmentation. Mortality profiles will also be estimated based on dental eruption and wear in order to determine the hunting strategies exploited by humans at the sites. Together, alongside

the data from the material culture analyses, should help to produce a more complete picture as to which tropical forest resources were exploited by Late Pleistocene to Holocene hunter-gatherers in the rainforests of Sri Lanka. I hypothesize that hunters were exploiting prime-aged arboreal and semi-arboreal prey, demonstrating specialized hunting strategies in lowland evergreen rainforests.

Fourthly, I will use ecological information gained from zooarchaeological identifications, alongside archaeobotanical research (including macrobotany and phytolith analysis), molluscan analysis, and geomorphology, to produce detailed ‘on-site’ palaeoenvironmental records for the site of Fa Hien-lena and Kitulgala Beli-lena. Together, with the records already existing for Batadomba-lena this will represent detailed palaeoecological insights, directly associated with the behaviour of Sri Lankan hunter-gatherers, from the earliest arrival of humans in the region, through the LGM, and into the Holocene. Based on work from Southeast Asia (Rabett, 2012), as well as existing stable isotope research in Sri Lanka (Roberts et al., 2017), I hypothesize that this will reveal reduction in tropical evergreen rainforest at the LGM, with an expansion of tropical evergreen rainforest during the Terminal Pleistocene and Holocene. When compared to insights into prey selection from the taphonomic analysis, as well as changes in stone and bone tool production, I hypothesize that human subsistence preferences will have altered in line with fluctuations in the tropical evergreen rainforest. Overall, I hypothesize, however, that specialized hunting of arboreal and semi-arboreal prey, alongside the use of tropical forest plants, persisted from the Late Pleistocene into the Holocene, through periods of significant climatic and environmental change.

The island of Sri Lanka potentially represents a unique case of Late Pleistocene human tropical forest colonization and occupation. The identification of specialized occupation of evergreen and





semi-evergreen lowland rainforest increases the diversity of tropical forest adaptations seen amongst populations of our species as it expanded beyond Africa. Not only did our species generalize in the use of montane tropical rainforests, peat swamp forests, dry tropical forests, coastal tropical forests, and evergreen and semi-evergreen tropical forests (Roberts and Petraglia, 2015), but individual populations were also able to specialize in the use of each of these habitats (Roberts and Stewart, 2018). In turn, these tropical forest environments are just some of the extreme environments, alongside deserts, palaeoarctic habitats, and high altitude environments, in which *H. sapiens* was able to hone specific adaptive strategies and cultural behaviours in order to thrive (Rabett, 2018; Roberts and Stewart, 2018). Producing more detailed understandings of how our species colonized the rainforests of Sri Lanka, how it exploited them, and how it persisted in them through periods of climatic variability, therefore promises to also enrich archaeological and palaeoanthropological understandings of the plasticity of our species as it came to colonize the planet, and the diversity of continents and environments it has to offer, during the Late Pleistocene.

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OPEN

Specialized rainforest hunting by *Homo sapiens* ~45,000 years ago

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Defining the distinctive capacities of *Homo sapiens* relative to other hominins is a major focus for human evolutionary studies. It has been argued that the procurement of small, difficult-to-catch, agile prey is a hallmark of complex behavior unique to our species; however, most research in this regard has been limited to the last 20,000 years in Europe and the Levant. Here, we present detailed faunal assemblage and taphonomic data from Fa-Hien Lena Cave in Sri Lanka that demonstrates specialized, sophisticated hunting of semi-arboreal and arboreal monkey and squirrel populations from ca. 45,000 years ago, in a tropical rainforest environment. Facilitated by complex osseous and microlithic technologies, we argue these data highlight that the early capture of small, elusive mammals was part of the plastic behavior of *Homo sapiens* that allowed it to rapidly colonize a series of extreme environments that were apparently untouched by its hominin relatives.

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There is growing evidence that *Homo sapiens* had a unique capacity to adapt to a diversity of extreme environments, both within and beyond Africa, when compared with other members of the genus *Homo*¹. Nevertheless, studies of migrations of our species into Europe, the Middle East, and Asia have often focused on its increased efficiency in hunting, butchering, and consuming medium-to-large game in open “savanna” settings^{2,3}. Alternatively, coastal settings have been highlighted as providing homogeneous, protein-rich resources that stimulated human evolution as well as migration beyond Africa from the Late Pleistocene^{4,5}. Focus on these environments has meant that small mammals have been neglected in discussions of the human colonization of new environments, despite the fact that a specialization in their procurement is often considered a feature of technological and behavioral “complexity” or “modernity” unique to our species^{6,7}. Concentration on Europe and West Asia in this regard has linked increased usage and capture of agile, but abundant, small mammals to human population growth or climatically driven crises associated with the end of the last glacial period⁶. Nevertheless, the onset and behavioral context of small mammal hunting in other parts of the world, and beyond temperate environments, has remained poorly studied.

From the Late Pleistocene onwards, our species inhabited a number of diverse environments as it dispersed beyond Africa. One of these environments, tropical rainforests, has been considered a barrier to human dispersal^{8,9}. This was mainly due to the fact that mammalian megafauna (> 44 kg¹⁰), thought to have been attractive to Late Pleistocene humans, and even driven to extinction as a

result of our species’ expansion^{11,12}, are lacking in these settings⁸. Nevertheless, in Sri Lanka, Southeast Asia, and Melanesia, as well as other parts of the world, the earliest evidence for human occupation is often associated with rainforest environments^{13–16}. In Sri Lanka, stable isotope evidence has demonstrated that humans relied on rainforest resources for over 30,000 years¹⁷, perhaps aided by the complex microlith and bone toolkits found at Late Pleistocene and early Holocene sites in the region^{15,16,18}. However, owing to a lack of detailed faunal analyses, it has remained unknown which food-stuffs sustained human populations during this time, as well as the hunting strategies employed to obtain them.

We apply new chronometric, taphonomic, archaeozoological, and artifactual analyses to the earliest dated archaeological site in Sri Lanka, Fa-Hien Lena (Fig. 1), previously dated to 38,000 years ago^{18–20}. Fa-Hien Lena documents the earliest fossil appearance of *H. sapiens* in Sri Lanka, and indeed South Asia, alongside small, quartz microlith technology, and a variety of pointed bone technologies^{18–20}. Rainforest mammals, reptiles, molluscs, and plant remains have been identified at the site^{18,20,21}. However, human exploitation of specific resources has yet to be directly demonstrated owing to a lack of systematic taphonomic study. Similarly, the early, enigmatic microlith and bone technologies discovered here and elsewhere in South Asia have undergone limited analysis, and their use and adaptive function have remained obscure^{19,20,22}. The results of our new multidisciplinary analyses document specialized, sophisticated hunting of semi-arboreal and arboreal prey taxa from ca. 45,000 years ago, in the tropical rainforest environments of Sri Lanka.

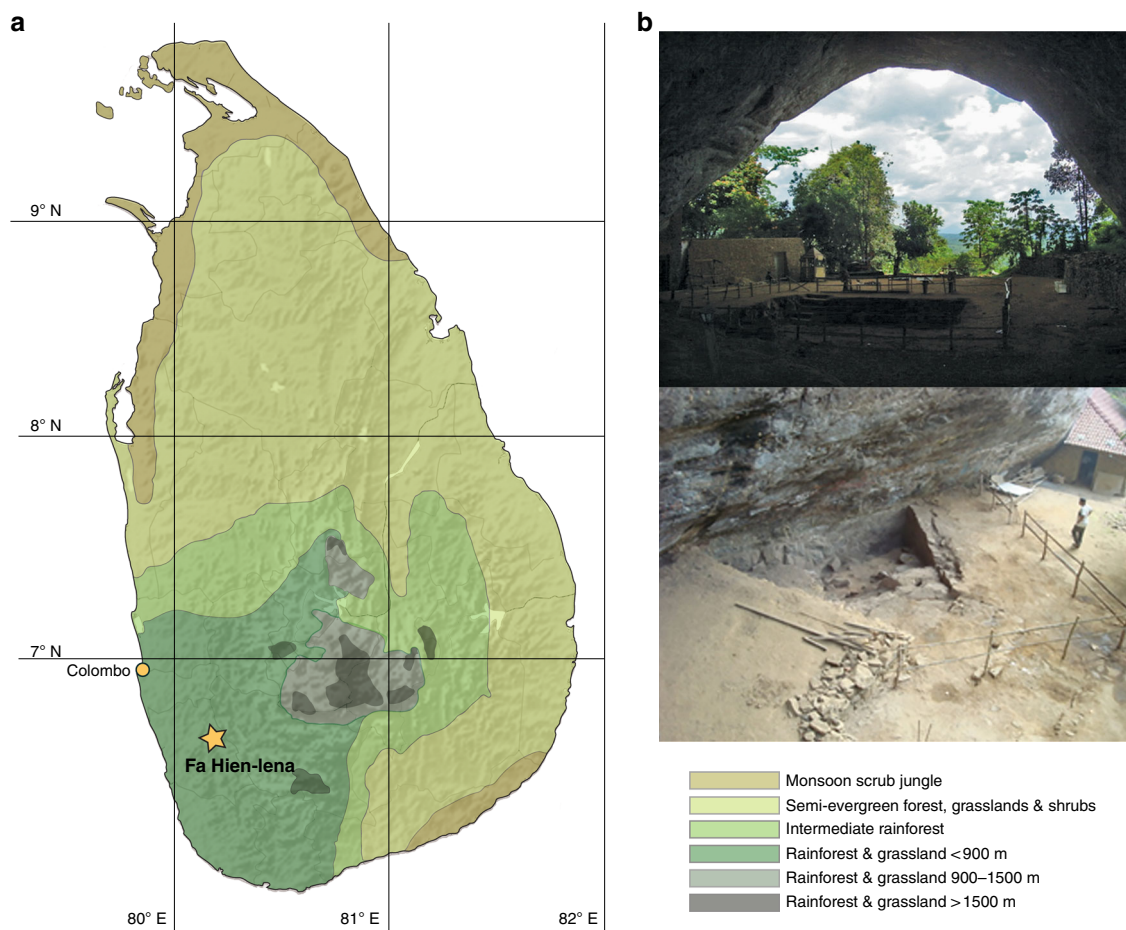


Fig. 1 Location of Fa-Hien Lena. **a** Map of Sri Lanka showing the location of Fa-Hien Lena and the country's vegetation zones^{44,45}. **b** Excavation in Fa-Hien Lena

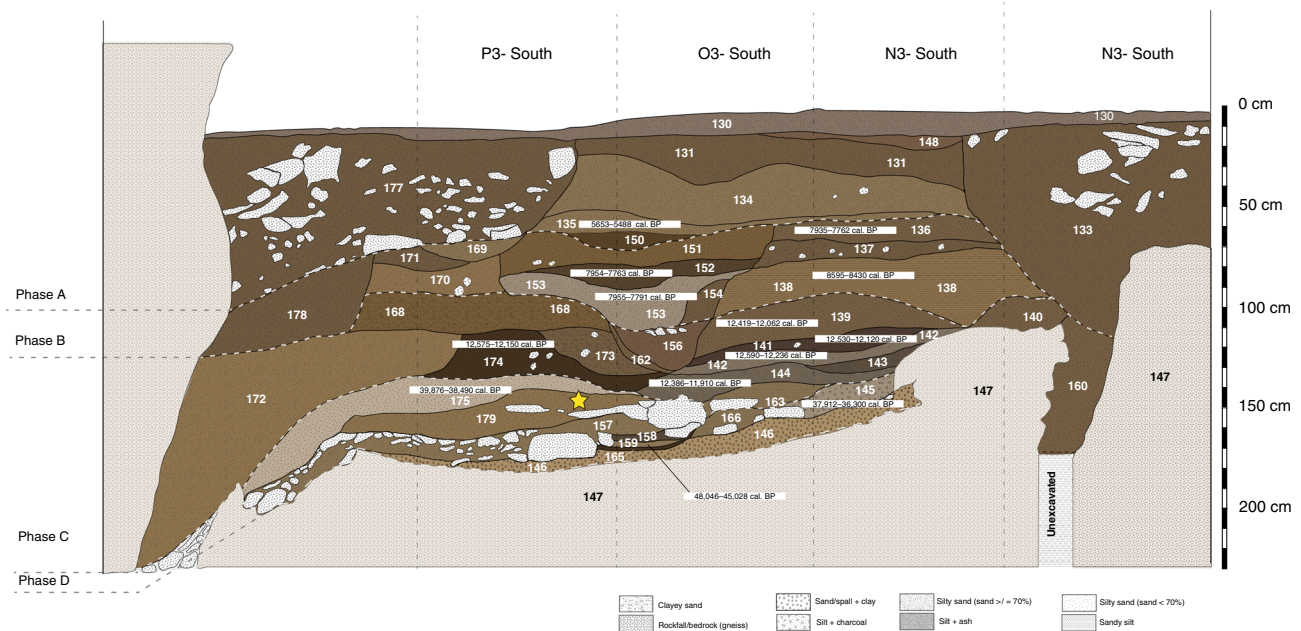


Fig. 2 Stratigraphy of Fa-Hien Lena. South wall, end of the 2010 excavation. The star indicates the approximate stratigraphic location¹⁹ of the fossils described by Kennedy²³

Results

Stratigraphy and chronology. We divide the dates available for the site into four distinct phases based on our new, and previous, excavations^{19,23}. The phases correspond to concentrations of charcoal, faunal remains, and artifacts, including osseous tools, shell beads, and quartz flakes (Supplementary Figure 1), and represent the major periods of human occupation of the cave. Phase D contains evidence for Late Pleistocene occupation of the cave from c. 48,000 to 34,000 cal. BP and probably included several episodes of occupation, each of which may have been relatively short-lived. Phase C spans the Terminal Pleistocene occupation from c. 13,000–12,000 cal. BP, while Phases B and A span the Early (8700 to 8000 cal. BP) and Middle (6000 to 4000 cal. BP) Holocene, respectively. One radiocarbon date falls outside these phases (29,120–27,870 cal. BP) and may represent a short-lived episode of human presence in the cave.

These phases also align with major lithostratigraphic changes (Fig. 2). The fill of Fa-Hien Lena consists of c. 170 cm of detrital sediment deposited above heavily weathered and karstified gneiss blocks. Phase D consists of pebbly loams and clayey and sandy silt deposits with laminated ash representing intermittent/episodic human occupation and colluvial inwash. The deposits yielded a variety of evidence for human activity, including heavily burned/calcined faunal remains, shell beads, bone tools, and other fragments, in addition to micromorphological analyses of sediments evidencing in situ burning (Supplementary Note 1). A roof fall episode appears to have contributed to the exceptional preservation of these deposits by sealing large parts of Phase D from later disturbance. Phase C, which contains the heaviest concentration of artifacts and human occupation debris in the stratigraphy, comprises of a rapidly deposited, heterogeneous mixture of dark colored, organic-rich sandy silty loams. Phases B and A are made up of light colored sandy silts and ash accumulations. For further detailed description, see Supplementary Note 1, Supplementary Tables 1–4, and Supplementary Figures 1–4.

Previous excavation in Fa-Hien-lena produced the oldest human fossils so far in Sri Lanka. Remains of a 5.5–6.5 years old child, mixed with remains of at least two infants as well as a

young adult female, were dated based on associated charcoal to 30,600 + 360 BP²³. These remains were found in layer 4 at the rear of the cave during the 1986 excavations¹⁹ (approximately represented by context 179 during our 2010 excavations) (Fig. 2). Overall, our new data confirm Fa-Hien Lena as the oldest site with *H. sapiens* fossils in Sri Lanka, and wider South Asia^{19,20}. They also indicate that Fa-Hien Lena now represents one of the earliest appearances of microlith toolkits and bone tool technocomplexes outside of Africa.

Zooarchaeology and taphonomy. Our detailed taphonomic and archaeozoological study of faunal remains at Fa-Hien Lena examined the adaptive context of the first humans on the island. We analyzed a total of 14,485 bone and tooth fragments from the site, 52.6% of which were identified to taxon (number of identified specimens, NISP = 7622). The full dataset can be found in Supplementary Note 2 (see also Supplementary Figures 5–16; Supplementary Tables 5–42). Small mammals (i.e., weighing less than 25 kg) overwhelmingly dominate the faunal assemblage starting from the earliest phase of occupation (c. 48,000–34,000 cal. BP). These animals, including carnivores such as the civet cat, account for more than 90% of the NISP, suggesting deliberate hunting from the Late Pleistocene until the Mid-Holocene (Fig. 3) (Supplementary Note 2). Reptiles, including pythons, colubrid snakes, and water monitors, and fish (mostly catfish and carp) are also present in all phases of site occupation. Several of the specimens identified could represent fauna from natural accumulations (e.g., murids and amphibians accumulated by raptors, 1.9% of the total NISP, see Supplementary Note 2). Other specimens, including birds such as swifts and swallows and squamates such as snakes and varanids, could represent the cave's natural faunal communities. However, the high percentage of burning (> 50% in Phase D) in squamate remains suggests that they were most likely utilized by the people that occupied the site (Supplementary Note 2).

There is no significant difference in the distribution of mammals based on body size from the Late Pleistocene to the Mid-Holocene (Supplementary Note 2). Large ungulates, including cervid, suid, and bovid are present throughout the

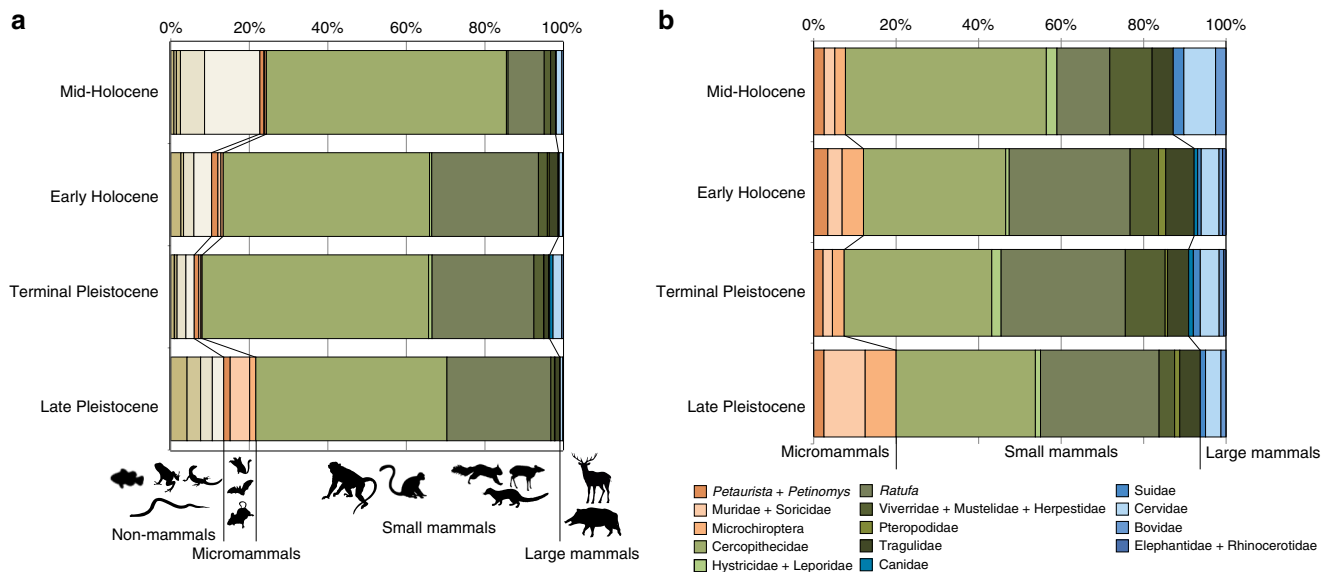


Fig. 3 Animal taxa identified in Fa-Hien Lena. Distribution of animal taxa identified in the different occupational phases of Fa-Hien Lena based on the number of identified specimens (NISP, **a**) and the minimum number of individuals (MNI, **b**). (Brown: non-mammals; orange: micromammals; green: small mammals; blue: large mammals)

stratigraphy but at very low frequencies (< 4%). Monkeys and tree squirrels overwhelmingly dominate the faunal assemblage in all phases of site occupation, accounting for more than 70% of the identified remains (or 82.4% of the total NISP discounting fauna most likely accumulated by non-human cave dwelling species). They represent 84.7% and 76.3% of the total number of identified specimens in the Terminal and Late Pleistocene layers, respectively (72.3% and 66.7% of the minimum number of individuals, MNI). Of the taxa identified in the Late Pleistocene layers, 48.7% are cercopithecoid monkeys. Deliberate targeting of monkeys continued until the Mid-Holocene, where cercopithecoids represent 61.1% of the number of identified bone and tooth fragments. Three cercopithecoid species are currently present in Sri Lanka: the cercopithecine *Macaca sinica* (toque macaque), the colobine monkeys *Trachypithecus vetulus* (purple-faced langur), and *Semnopithecus priam* (tufted gray langur). These species occur sympatrically and all were identified in the site. Macaques slightly outnumber the leaf monkeys in the faunal assemblage (Supplementary Note 2).

Mortality profiles based on dental eruption and wear suggest that prime-aged adults were deliberately targeted. This, and the fact that the identified monkey species are today mostly arboreal and rarely venture to the ground^{24,25}, suggests that they were most likely captured by targeted hunting. Trapping usually results in mortality profiles similar to those found in natural populations^{26–28}. The presence of bone points and microliths from the outset of site occupation hints at the possible use of projectile technology to hunt arboreal prey (see below, and Supplementary Note 3, Supplementary Figures 17–19, and Supplementary Tables 43 and 44). Modern Southeast Asian hunter-gatherer communities still rely on the use of projectile weapons, including darts and blowpipes, to target arboreal and semi-arboreal taxa^{29–31}. The archaeological bone points are consistent in size and breakage patterns with such uses. Regardless of method of capture, entire monkey carcasses were brought and processed in the site as revealed by the pattern of skeletal part abundance (Supplementary Note 2).

Bone fragments with anthropic modification, ranging from burning to butchery marks, were recovered in all phases of site

occupation. Butchery marks were recorded on a total of 92 bone fragments (0.64%), the majority of which were from small mammals (92.2%) (Supplementary Note 2). The Late Pleistocene layers yielded a total of nine (0.7% of NISP) bone fragments with clear evidence for butchery, including squirrel, otter, and civet cat long bones from the oldest occupation deposit of the site (Fig. 4). The placement of the cutmarks, both in the shaft surface and the distal epiphyses, is suggestive of a carcass processing sequence that involved disarticulation and defleshing³². Burnt and calcined bone fragments represent 19.7% of the total specimens studied (23.9% of the Late Pleistocene assemblage). A high proportion of the small mammal (17.1%) remains identified at the site exhibit evidence for burning, including 16.1% of the monkey remains.

Bone tool industry. Primates and giant squirrels appear to have been targeted not just for subsistence, but also for technological production. A total of 36 bone specimens with surface modifications consistent with systematic tool manufacture were recorded in the Late Pleistocene layers (Phase D) of the site (1.3% of the NISP). These consist of 10 fragments of finished implements, including proximally hafted unipoints, mesially hafted bipoints, and small geometric bipoints. The rest are fragments that represent either waste pieces or tool blanks. These specimens are characterized by the presence of heavy surface and/or edge polish and striations or grinding marks. In situ tool production accounts for the high level of fragmentation of cercopithecoid bones in all levels of site occupation, but most notably in the Late Pleistocene layers (Supplementary Note 2).

The osseous tools from the Late Pleistocene layers of the site appear to have been manufactured exclusively from cercopithecoid long bone fragments, save for one worked macaque canine recorded from the earliest phase of site occupation (context 253) (Fig. 4). Tools and artifacts made from large ungulate bone, teeth, and antler only start to appear during the Terminal Pleistocene. Most of the bone points examined exhibited evidence for damage consistent with high velocity impact (four out of the five points recorded in Phase D, e.g., Fig. 4)³³, which, in addition to what appears to be deliberate targeting of prime age adults, further

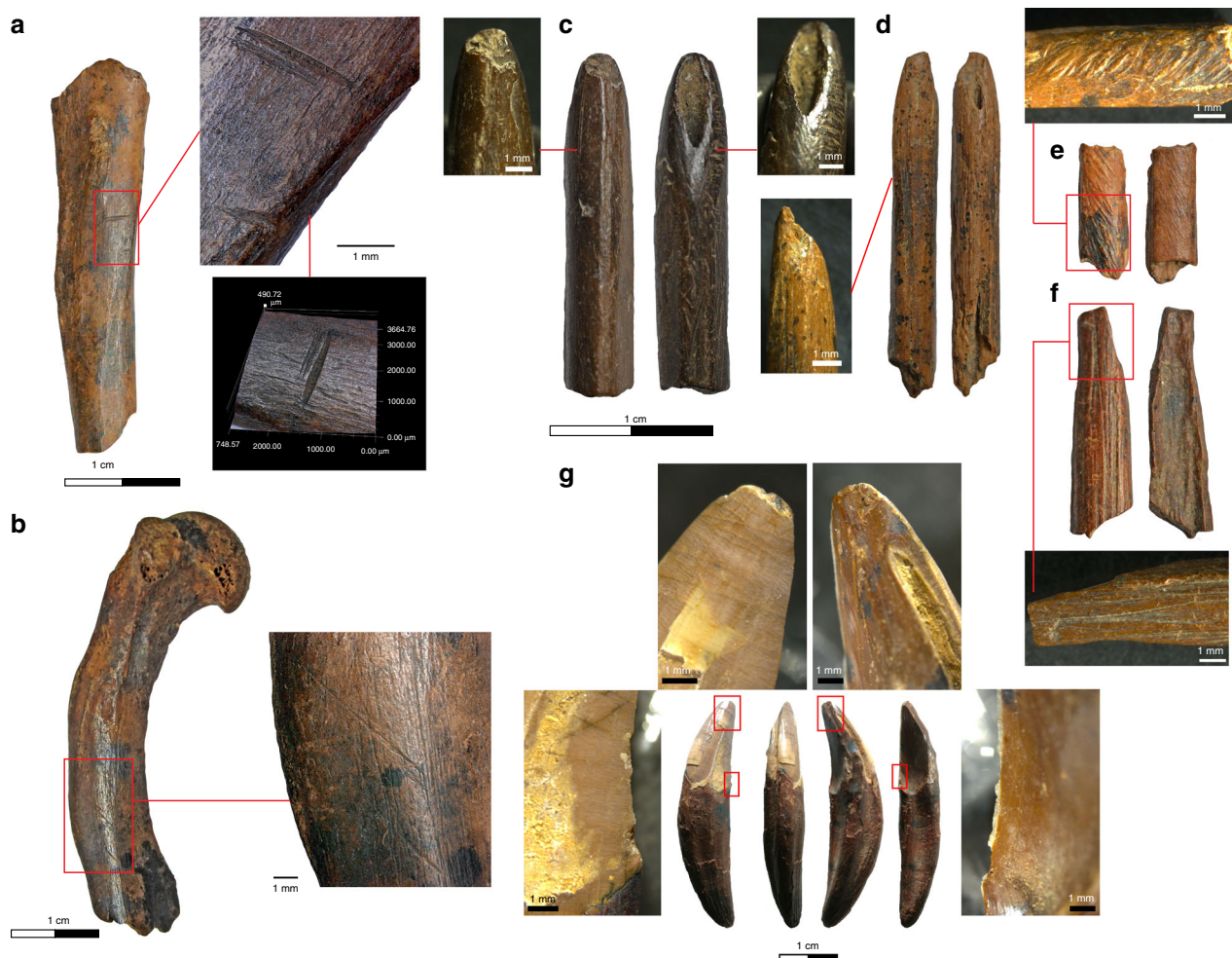


Fig. 4 Specimens with anthropic modifications from the Late Pleistocene layers of Fa-Hien Lena. Bone fragments with evidence for butchery and osseous tools and artifacts from the earliest phase of occupation at Fa-Hien Lena. **a** Cutmarks on a grizzled giant squirrel (*Ratufa*) tibia. **b** Cutmarks on an otter (*Lutra*) humerus. **c, d** Cercopithecoid monkey fibula points with evidence for shaping (ground) before high-pressure tip use. **e** Monkey distal fibula shaft fragment with grinding marks. **f** Worked monkey femur shaft fragment. **g** Worked macaque canine showing damage from use in cutting (on sides) and pressure/piercing on tip

suggests that projectile hunting, rather than trapping, was utilized in the exploitation of small semi-arboreal and arboreal game.

Discussion

The consistently high percentage of arboreal small mammal taxa in all phases of occupation in Fa-Hien Lena is unheard of even among modern ethnographic groups hunting in tropical rainforest environments^{20,34}, with perhaps one exception³⁵. Even with access to rifle technologies and wire cord and snare traps, modern foragers never show such a bias³⁴. Late Pleistocene hunting of arboreal primates has also been demonstrated at the Niah Caves, Borneo from 50,000 to 35,000 years BP. However, here, in contrast to Fa-Hien Lena, humans seemingly primarily relied on large ungulates as their main source of protein²⁸. This, alongside associated evidence from what is, to our knowledge, one of the earliest bone tool assemblages in South and Southeast Asia (contemporaneous with the bone tools from Niah Caves dated between 50,000 and 35,000 years BP³³), and also one of the earliest beyond Africa, implies highly tuned hunting abilities in tropical rainforest settings upon arrival in this part of the world. Moreover, despite targeting prime age adults, these human populations were able to exploit primate and giant squirrel taxa, often considered to be rainforest game types that are among the

most vulnerable to overhunting³⁶, from ~45,000 to 4,000 years ago. This suggests close knowledge of life cycles, territories, and sustainable hunting strategies³⁷.

Discussions of Late Pleistocene dispersals of *H. sapiens* beyond Africa have tended to focus on human reliance on large, mammalian megafauna that are often linked to open grassland or mixed woodland and grassland environments^{8,11}. Alternatively, scholars have focused on reliable coastal resources as providing adaptive corridors for a rapid dispersal around the Indian Ocean, through Southeast Asia, and into Australia^{4,5}, and also into the Americas³⁸. Our current data, demonstrate instead that some of the earliest known *H. sapiens* in Sri Lanka, and indeed in the South Asian tropics, focused on the specialized hunting of small semi-arboreal and arboreal mammals in tropical rainforests. Traditionally, the use of such difficult-to-catch resources has been associated with a “broad spectrum” revolution in the face of growing populations and climate change. However, continued emphasis on prime age animals across over 40,000 years, rather than a broadening of capture strategy, implies no such stress in the tropical rainforests of Sri Lanka. Furthermore, while stable isotopic data from human and faunal tooth enamel in the Wet Zone of Sri Lanka highlights subtle environmental changes from the Late Pleistocene to the Holocene, the persistence of Wet Zone and Intermediate Zone rainforest, as well as human reliance on

this forest^{17,39}, suggests these environments did not reach carrying capacity.

As a consequence, the utilization of these energetically expensive resources developed in the absence of resource pressure, documents the behavioral and technological flexibility of *H. sapiens*. These complex subsistence strategies appear to be part of the adaptive ecological plasticity of our species that enabled it to inhabit diverse Late Pleistocene habitats across the world¹. The primary niche of non-*H. sapiens* hominins within and beyond Africa appears to be diverse forest and grassland mosaics in the vicinity of rivers and lakes^{40,41}. By contrast, following its evolution in Africa c. 300 ka⁴², our species came to occupy higher-elevation niches than its hominin predecessors, as well as deserts, palaeoartic settings, and tropical rainforest habitats stretching across Asia, Melanesia, and North, Central, and South America¹. Moreover, it was even able to alter and manage environments, such as tropical forests, to meet its own subsistence and cultural needs through ever-intensifying niche-construction^{39,43}. Detailed paleoecological and archeological analysis, such as that presented here, offers to yield more insights into the variety of cultural and subsistence strategies that facilitated the eventual colonization of all of the world's continents, and resilience to increasingly extreme Pleistocene climatic fluctuations, that left *H. sapiens* the last hominin standing on the face of the planet.

Methods

Chronology and thin section micromorphology. Fa-Hien Lena (80° 12' 55" E, 6° 38' 55" N) is located in Sri Lanka's Wet Zone region, near the town of Bulathsinhala, some 75 km southeast of Colombo in a lowland evergreen and semi-evergreen rainforest environment^{44,45}. The cave, on the slope of a gneiss cliff, has a c. 30 m by 20 m east-facing entrance, an interior that extends c. 10 m into the cliff, and two main chambers (termed shelters A and B). First recorded by S.U. Deraniyagala in 1968, Fa-Hien Lena was systematically excavated over several seasons from 1986 to 1988 by W.H. Wijeyapala, and from 2009 to 2012 by a team led by O. Wedage, S.U. Deraniyagala, and N. Perera. Shelter A, the larger of the cave's chambers, was excavated to a depth of over 6 m. However, the shelter's archaeological deposits are disturbed by recent Buddhist constructions. Shelter B, on the other hand, produced a sequence of archaeological deposits spanning from what appears to be the earliest occupation of Sri Lanka by our species (previously dated to 38,000 cal. BP^{19,20}) through to the Middle Holocene.

This paper presents the results of the analyses of materials from 2009 to 2012 excavations. We added to existing radiocarbon dates and present a revised stratigraphy for the site. Together with dates previously published^{19,23,46,47}, which we calibrated using OxCal 4.3⁴⁸, we present a total of 30 radiocarbon dates (Supplementary Tables 1–4) that are now available for Fa-Hien Lena, enabling detailed phasing for the site.

A set of undisturbed sediment samples were collected from the excavated profile in clear polyurethane boxes. Sample boxes were labeled, photographed, and plotted on the profile drawing before removal from the profile. Four of these samples, all from Phase D sediments, were selected for micromorphological analysis (Supplementary Figure 2), aiming to understand the depositional history and to access the taphonomic integrity of these earliest occupation deposits. Sample processing, at the Thin Section Micromorphology Laboratory, University of Stirling included air-drying and impregnation with polyester (polylite) resin (<http://www.thin.stir.ac.uk/>). c. 30-µm thick, covered, large format thin sections (7.5 × 11 cm) were manufactured from the hardened impregnated blocks (sample code FH). Thin sections were observed with a polarizing microscope at magnifications of ×12.5 to ×400, using plain polarized (PPL), cross-polarized (XPL), and oblique incident light (OIL). The relative abundance of sediment components was estimated using standard semi-quantitative estimation charts^{49,50}.

Zooarchaeology and taphonomy. We analyzed faunal remains recovered from the 2009 and 2012 excavations of Fa-Hien Lena. All bone fragments from sedimentary contexts with secure radiocarbon dates (including those from deposits sandwiched by dated layers) were included in the analysis. All specimens, including diaphyses and rib shafts, were sorted, counted, and measured (length, width, and thickness) using a digital caliper (Mitutoyo 500–463). Identified specimens were recorded in detail using codes for anatomic zones⁵¹ (e.g., Supplementary Figure 5) that allow the description of bone preservation/fragmentation patterns. Diagnostic dental and skeletal elements were identified to the highest possible taxonomic level using vertebrate comparative collections from the Laboratory of Comparative Anatomy of the *Muséum national d'Histoire naturelle* (MNHN) in Paris and photographs from the mammalian collections of the Field Museum of Natural History and American Museum of Natural History. Following von den Driesch⁵², individual

dental specimens and specific anatomical features of diagnostic skeletal elements were measured to differentiate between closely related taxa. The naming of identified taxa follows the nomenclature for mammalian species of Wilson and Reeder⁵³. The taxa identified in the sites were assigned to size class based on live weight (modified from refs. ^{54,55}): (a) micromammals: 100 g to 1 kg, (b) small mammals: 1 kg to 25 kg, (c) large mammals class 1: 25 kg to 200 kg, (d) large mammals class 2: 200 kg to 1000 kg, and (e) large mammals class 3: > 1000 kg.

All fragments were examined for natural, animal, and anthropic modifications, including weathering^{56,57}, abrasion⁵⁸, burning, staining, and butchery marks³². Bone surface modifications were recorded/observed using an Olympus BX53 light microscope and a Keyence VHX-6000 digital microscope. Burnt bone fragments were identified based on color^{59–61}. They were distinguished into different classes based on the degree of burning⁵⁶: (1) partially burnt, (2) charred (blackened), and (3) calcined (partial and complete calcination). Burnt bones were quantified by determining the percentage of the total bone fragments that is comprised of burnt specimens^{62,63}.

The minimum number of element (MNE) and minimum number of individual (MNI) counts were calculated following a modification of Dobney and Rielley's⁵¹ zonation system. This system is based on the recording of morphologically distinct zones in a skeletal element. The MNE was taken as the total number of non-repeatable zones (i.e., greater than 50% of the diagnostic zone present) for every skeletal element of a taxon. The highest MNE value, considering side and age (epiphyseal fusion and dental wear⁶⁴), was used to estimate the MNI. The MNE counts were converted to minimum animal unit (MAU) values by taking into account the number of times the element occurs in the skeleton. The normed MAU values (% MAU) were used to compare skeletal part representation in the different phases of cave occupation⁶⁵.

The length and circumference of long bone fragments were also recorded in relation to complete specimens to measure the extent of bone fragmentation in the assemblage. Long bone fragments were assigned the following fragment circumference and length scores^{66,67}: (1) fragments with less than half of the circumference/length of the complete specimen, (2) fragments with more than half of the circumference/length of the complete specimen, and (3) fragments with the complete circumference/length of the complete specimen.

Artifact analysis. The technological study of the lithic assemblages of Fa-Hien Lena was carried out following the *chaîne opératoire* concept^{68,69}, a methodological framework that defines the reconstruction of the various processes of flake production from the procurement of raw materials, through the phases of manufacture and utilization until the final discard. The *chaîne opératoire* concept provides systematic sequences of the flaking activities in which is possible to determine the temporal phase and the position of the artifact produced⁷⁰. The lithic material is composed of 5070 items (Supplementary Tables 43–44). The predominant raw material is quartz, which is abundantly available in the streams nearby.

Few chert blanks were also found and include: a silet flake fragment in context 131 (Phase A); two flakes and a fragment in context 136 (Phase B); a flake fragment in context 141; and one flake and one blade from context 248 (Phase C).

For the analysis of osseous artifacts, the materials were examined using a Zeiss Stemi 508 stereomicroscope fitted with an AxioCam 105 camera. Taphonomic and anthropogenic alterations were identified based on published works^{58,71–78} and mapped onto photographs taken with a Canon digital SLR camera.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The authors declare that all data supporting the findings of this study are available upon request from the authors. The artifacts and faunal remains from the Fa-Hien Lena excavations are curated at the Department of Archeology, Government of Sri Lanka, under the site code BYP and the suffixes 10, 11, and 12 (denoting the year of excavation). Some materials remained housed at the Max Planck Institute for the Science of Human History to be returned to the Department of Archeology, Government of Sri Lanka by the end of 2019. All of the data reported in the paper are presented in the main text or in the Supplementary Notes, Tables, and Figures.

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Author contributions

O.W., N.A., M.D.P., and P.R. designed the research; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.B., M.D.P., and P.R. collected the data; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.P., N.B., M.D.P., and P.R. analyzed the data; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.P., N.B., M.D.P., and P.R. wrote the paper.

Additional information

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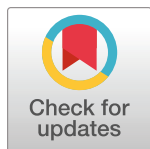
RESEARCH ARTICLE

Microliths in the South Asian rainforest ~45-4 ka: New insights from Fa-Hien Lena Cave, Sri Lanka

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Data Availability Statement: All relevant data are within the paper and its Supporting Information files. The lithic material is located in the Department of Archaeology, Government of Sri Lanka, Colombo, Sri Lanka where they are accessible to others, following permitting requests, in a permanent repository. While there are not specific accession numbers for each artefact, artefacts are stored under the site code 'FH' with clear contextual designators correlating to the phasing described here.

Abstract

Microliths—small, retouched, often-backed stone tools—are often interpreted to be the product of composite tools, including projectile weapons, and efficient hunting strategies by modern humans. In Europe and Africa these lithic toolkits are linked to hunting of medium- and large-sized game found in grassland or woodland settings, or as adaptations to risky environments during periods of climatic change. Here, we report on a recently excavated lithic assemblage from the Late Pleistocene cave site of Fa-Hien Lena in the tropical evergreen rainforest of Sri Lanka. Our analyses demonstrate that Fa-Hien Lena represents the earliest microlith assemblage in South Asia (c. 48,000–45,000 cal. years BP) in firm association with evidence for the procurement of small to medium size arboreal prey and rainforest plants. Moreover, our data highlight that the lithic technology of Fa-Hien Lena changed little over the long span of human occupation (c. 48,000–45,000 cal. years BP to c. 4,000 cal. years BP) indicating a successful, stable technological adaptation to the tropics. We argue that microlith assemblages were an important part of the environmental plasticity that enabled *Homo sapiens* to colonise and specialise in a diversity of ecological settings during its expansion within and beyond Africa. The proliferation of diverse microlithic technologies across Eurasia c. 48–45 ka was part of a flexible human 'toolkit' that assisted our species' spread into all of the world's environments, and the development of specialised technological and cultural approaches to novel ecological situations.

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Introduction

In the last decade, growing archaeological and palaeoenvironmental evidence has documented the use of tropical rainforest resources by *Homo sapiens* in several locations in South Asia, South East Asia, and Melanesia between 45,000 and 36,000 years ago [1–8]. There have also been more tentative suggestions of tropical rainforest adaptations by our species at earlier dates in Africa [9–11] and Sumatra [12]. Scholars had previously considered these environments to be barriers to human forager occupation, due to the scarcity of carbohydrate-rich plants, limited fat and protein-rich fauna, and difficulties of movement and thermoregulation [13–16]. Instead, most discussions of the evolution and migration of our species focused on the medium- and large-sized game available in grassland or savanna settings [17–19] or protein rich maritime resources available in coastal settings [20,21]. Archaeological evidence for the recurrent exploitation of tropical rainforests has also indicated that these environments played a central role in human adaptations [5–8]. The wide use of ecological settings by our species demonstrates increased levels of ecological plasticity, enabling the spread of human populations into a diversity of ‘extreme’ environments during its expansion within and beyond Africa [22,23].

The island of Sri Lanka, at the southern tip of South Asia, has emerged as a particularly important area for the investigation of prehistoric hunter-gatherer adaptations and technological strategies used in tropical rainforest ecosystems. Caves and rockshelters excavated in the modern Wet Zone rainforest of Sri Lanka since the 1950s (Fig 1) have yielded long stratigraphic sequences, with well-preserved organic plant and animal remains in Late Pleistocene and Holocene contexts [1,24,25]. The earliest human fossils of South Asia are found in the Sri Lankan caves and rockshelters, in levels dated to c. 45,000–36,000 cal. years BP [26,27]. Stable isotope analysis of human and animal tooth enamel, alongside zooarchaeological and archaeobotanical analysis [25,26], has highlighted that these human foragers relied almost entirely on rainforest resources for their subsistence needs between 36,000–3,000 cal. years BP [5,7]. What is less clear, however, is the range of technological strategies that these populations used to enable their dedicated rainforest subsistence practices, and how adaptations may have varied through time. Analysis of bone tools found at the site of Batadomba-lena has suggested that they were used as components of composite projectiles, in traps, or even as freshwater snail picks [28]. Stone tools, predominately made from small flakes of quartz, occur in much greater abundance in these early rainforest occupation sites but their interpretation has typically focused on simplistic typological comparisons, entraining them into competing models of human dispersal [29–31]. More detailed appraisal of lithic technology from Batadomba-lena suggests that further evaluation of technological variability is warranted within the early rainforest occupation sites of Sri Lanka [32], alongside a wider framework for interpretation of the origins and uses of these lithic industries.

Here, building on the new multidisciplinary analysis of the Fa-Hien Lena sequence [26], we report the first detailed analysis of lithic technology from the site Fa-Hien Lena, based upon excavations conducted in 2009, 2010, and 2012 [26] (Fig 1). The earliest lithic industries at this site are associated with the oldest skeletal evidence for *H. sapiens* in South Asia, found in a rainforest context [26]. Below we review historical and current debate regarding microlithic stone tool industries as well as available evidence for the colonisation of rainforest habitats by *H. sapiens*. Following a description of the stratigraphy and chronology of Fa-Hien Lena, we present a detailed assessment of the nature of lithic technology and examine patterns of change through time. We place these results in their regional context, through comparisons with the well-studied Sri Lankan site of Batadomba-lena [32,33], as well as more broadly across South Asia. We also evaluate our results within wider discussions of the emergence of microlithic

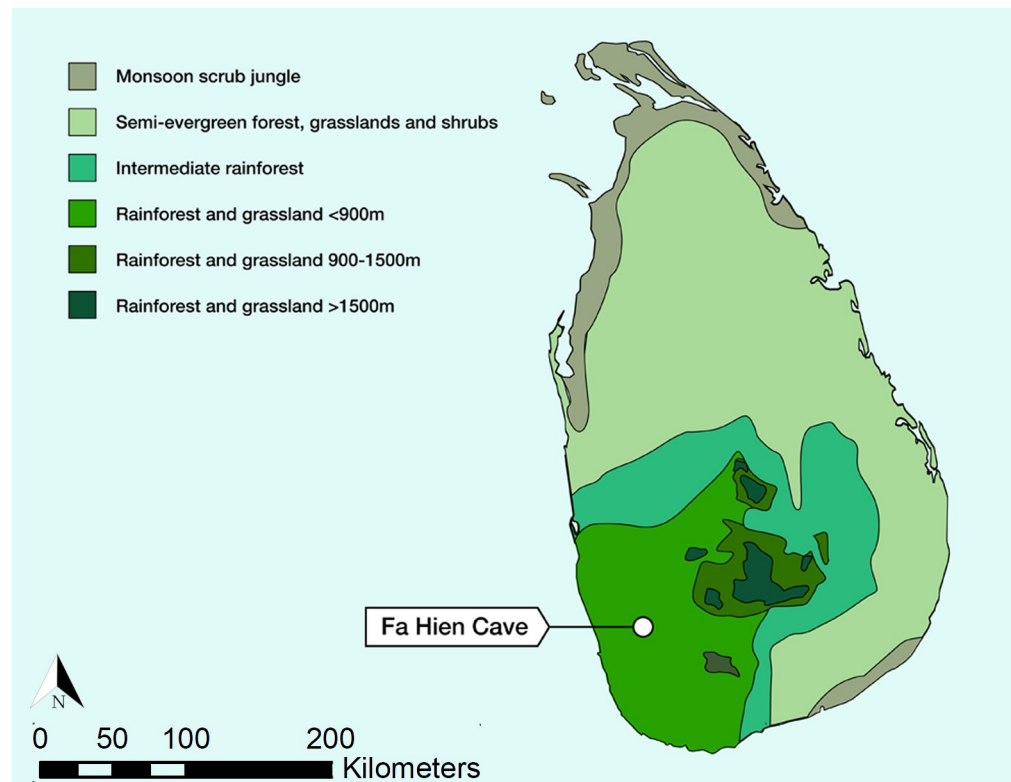


Fig 1. Map of the position of Fa-Hien Lena relative to Sri Lanka's vegetation zones.

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technologies and their role in adaptation to diverse ecological contexts, with a particular focus on rainforest environments.

Background

Defining the microlithic

Defining microlithic technology is not straightforward, as no single 'one-size-fits-all' definition can readily encompass all archaeological assemblages to which the term has been applied without losing analytical value. Half a century ago Clark defined a series of technological modes [34] as part of a framework rooted in the European record that would help organise and understand global patterns in Palaeolithic technological variability. In this system, microlithic technologies comprised 'Mode 5', yet this definition conflated aspects of production, focusing on small flakes and blades as blanks for retouched tools, and use, with the implication that these tools were used in composite, hafted tools. While undoubtedly this definition has proven to be both useful and influential, including its application within South Asia, a growing body of evidence suggests that definitions of the microlithic based on their expression in Europe may not be appropriate for other regions of the world [35–40].

The creation of criteria for identifying microlithic technologies based upon characteristics of individual archaeological sites or regions is problematic. Pargeter [40] breaks the focus on small, backed bladelets into its three component elements focused purely on stone tool reduction (excluding assumptions of use): 1) systematic production of small flakes from fine grained stone; 2) use of backing (abrupt) retouch, including the production of geometric forms; and 3) bladelet production from prismatic cores. More recently, Pargeter and Shea [41] examined

long-term trends in the practice of miniaturisation of lithic technology and presented a number of useful criteria from archaeological, experimental and ethnographic studies to clarify and constrain the use of terms such as microlithic (summarised in Table 1).

Here, we retain the term microlithic, and use it specifically to refer to stone tool technologies dedicated to the production of small lithic artefacts, conforming to the criteria proposed by Pargeter and Shea [41] (Table 1), rather than on the explicit focus on small backed tools. Indeed, microlithism need not necessarily include backed tools [41–43]. Following the demonstration of the bimodal distribution of blade sizes in southern India [44], we employ a 40mm size threshold and describe flakes, blades (bladelets), and retouched tools smaller than 40mm as microlithic. In a similar manner, cores that have been systematically exploited to produce blanks below the 40mm threshold are described as microlithic. While the appearance of bladelets and backed artefacts can be a feature of microlithic technologies, their absence is not considered critical for attributing lithic assemblages to microlithic technologies.

Antiquity of the microlithic in South Asia. In the middle of the 20th century, the African terminology for describing prehistoric stone tool industries was employed in South Asia, differentiating the Early, Middle and Later Stone Age (e.g. [45]). Within this scheme, Later Stone Age assemblages broadly corresponded to microlithic technologies. The adoption of the European terminology of Lower, Middle, Upper Palaeolithic, and Mesolithic in South Asia from the 1970's onwards led to a more direct parallel being drawn between the microlithic industries of South Asia and the Mesolithic of Europe. This led to the longstanding use of the term 'Mesolithic' to encompass microlithic industries (e.g. [1,46]), as well as the argument for a recent antiquity of microlithic technologies, thought typically to date to the early Holocene or the terminal Pleistocene. Given the scarcity of chronometric dates, this viewpoint persisted in spite of evidence for microlithic assemblages older than 25 ka in India [47] and as early as c. 30 ka in Sri Lanka [1].

During the past decade a growing number of sites associated with chronometric ages have clearly demonstrated the Pleistocene antiquity of microlithic assemblages in South Asia. In

Table 1. Criteria for identifying miniaturised lithic reduction practices (after Pargeter and Shea [41]). Given that the term 'microlith' is often interchangeable with backed geometrics in the South Asian Palaeolithic literature, disambiguation is important.

Type	Criteria
Targeted Production of Small Tools	As a reductive medium, flaking at many scales can produce small artefacts. Identification of dedicated focus on small tools can include the following: a) Demonstrate that small size is not a restriction of clast size availability through raw material availability; b) Preclude impact of reduction intensity as key driver of size by illustrating systematic core reduction and management practices amongst small artefacts; c) Exhibit selection of small flake blanks for retouched tools.
Small tool sizes	Inter-regional comparisons suggest artefacts <50mm can reflect systematic production of small tools.
Production Methods	Freehand flaking becomes more difficult amongst cores <20mm, whereas bipolar flaking can remain productive for cores <10mm.
Microflake vs Microblade	Both flake and blade production can feature amongst small tool technologies, rather than either being a prerequisite; while bladelets may increase the production of cutting edge on regular sized/shaped blanks, the application of laminar methods may be limited by differences in utility in individual artefacts requiring higher replacement rates and higher risks of bending fractures, leading to a preference for homogeneous materials.
Tool use	Backing is a prominent form of retouching of small tools, and may improve the strength of hafted pieces; however, unretouched small flakes can also make efficient hand tools and hafted tool inserts.

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India, these include studies from South India (e.g. Jurreru Valley ~35 ka [48–49]), Central India (e.g. Mehtakheri ~44 ka [50]; Patne >25 ka [47]), West India (e.g. Buddha Pushkar ~28 ka [51]), North India (e.g. Middle Son Valley 55–47 ka [52]) and East India (e.g. Kana ~42 ka [53]). Recent reappraisal of the chronology of microlithic assemblages from Sri Lanka, clearly demonstrates a comparable antiquity for microlithic industries at Batadomba-lena (~36 ka) [25] and Kitulgala Beli-lena (~33 ka) [1,5,54]. Critically, renewed dating programs at these Sri Lankan sites are extending the chronological range of these industries, including at Fa-Hien Lena, the site with the earliest confirmed ages for human occupation on the island [5].

Historically, microlithic technologies in South Asia were argued to have developed locally from a distinct Upper Palaeolithic antecedent (e.g. [55]). However, the recognition of a shared African ancestry for all modern humans, as opposed to a strong multi-regional model, has led to a focus on microlithic industries as potential markers of the rapid expansion of *H. sapiens* populations through coastal environments or grassland corridors [29,50,56]. This is, in part, due to the place of microliths within a package of behaviours thought to be unique to ‘modern’ humans, emerging in Africa by 80–60 ka [56–58]. Such models, rooted in mtDNA studies of contemporary populations and simplistic lithic comparison [57,58], have been subject to sustained critique on a number of grounds. Most crucially here, technological diversity of microlithic assemblages between Africa and Asia was ignored in favour of asserting a typological ubiquity [32,33]. An absence of microlithic industries around much of the Indian Ocean Rim also makes suggestions of cultural inheritance between Africa and South Asia difficult to support [30]. Nuclear genome research, as well as fossil discoveries across Asia [59,60], has also complicated the association of microlith toolkits with the first members of our species in different parts of the world. Finally, the appearance of backing and microliths in Uluzzian industries in Italy, which are amongst the earliest microlithic industries outside of Africa and are associated with *H. sapiens*, clearly suggests that microliths were not the sole preserve of foragers in woodland and savanna settings [61–63].

In their review of the global appearance of backed microliths, Clarkson and colleagues [39] argue that convergent evolution in different environmental and cultural settings, not a single origin and dispersal [58], offers a better explanation of the global origins of microliths. They argue that microliths offered a range of functional advantages, including transportability, efficiency of raw material use, ease of manufacture and maintainability, and advantages specific to backed pieces, including standardisation, haftability and reliability, that would promote their adoption by numerous, unrelated populations. In several regions in India, the innovation of microlithic tool kits appears to be rooted in previous Middle Palaeolithic technologies [44,52]. In both these Indian examples, the appearance of microliths is linked to the combination of increasing demographic pressures and worsening climatic conditions. Elsewhere, it has been argued that demographic pressures have played a major role in technological development among our species [64]. In contrast to the contexts in which they have been found in the rest of the world, in Sri Lanka microlithic technologies occur in tropical rainforest environments, often argued to be more stable ecosystems in the face of climatic change [1,46]. However, despite the significance of microliths in these contexts, detailed discussions of temporal changes in their production, morphology, and the context of their use have been limited to isolated studies [1,32].

Fa-Hien Lena Cave

Fa-Hien Lena cave, one of the largest caves in Sri Lanka, is situated in Yatagampitiya village (80°12'E, 6°38'N), near the Bulathsinhala Divisional Secretariat Division in the Kalutara District of the Western Province (Fig 1), at approximately 130 meters above mean sea level. It is a

shallow rockshelter containing prehistoric habitation, situated next to a large domed cave [24,46,65]—formed in an almost vertical southwest-facing cliff of Proterozoic gneiss of the Highlands Complex [66]. The humus-stained cliff containing these caves drops from a forested summit to the banks of a small stream. The caves are situated at the gradient break between the steep rock cliff and the lower gradient colluvium slope (Fig 2). Large boulders on the forested colluvial slopes below the caves provide evidence for relatively recent rockfall and retreat of the steep gneiss cliff [24,46,62,65].

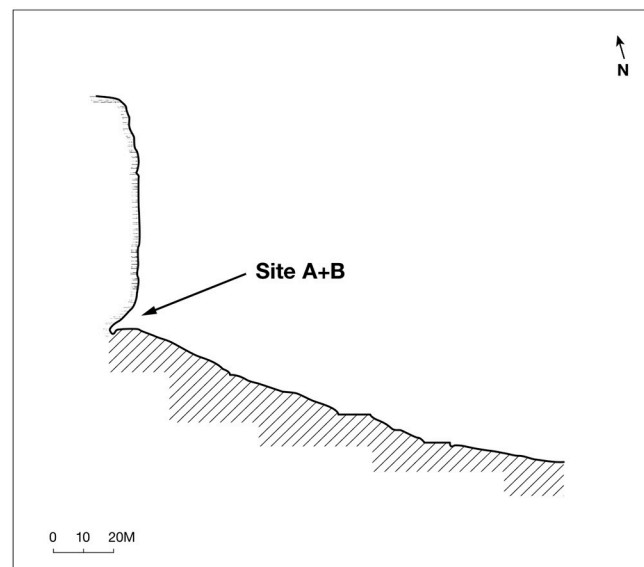
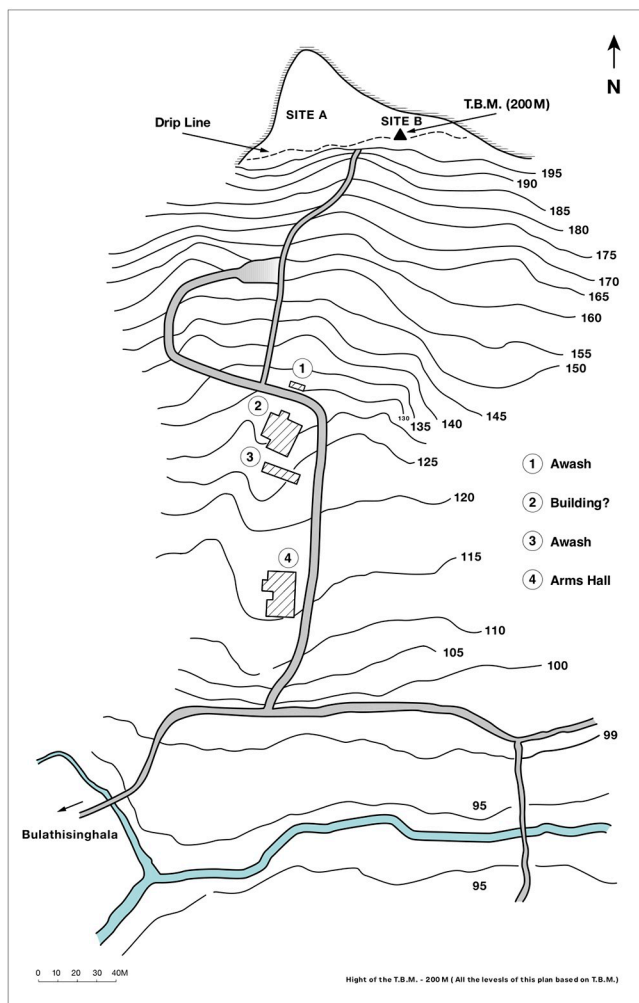
The first excavations at Fa-Hien Lena Cave occurred between 1986–1988 in two main areas, Cave A and Shelter B, with the aim of understanding the cultural sequence of the cave (Fig 2) [24]. Cave A, the larger one of the two, was first excavated to a depth of over 6 m. It yielded deposits of what appears to be roof-fall flakes and decaying bedrock throughout the profile, without any definitive trace of early human habitation [24,26]. Shelter B, a smaller subsidiary rockshelter located approximately 20m east of the main Cave A chamber, proved to be far more productive. Excavations conducted in 1986 identified five strata, with excavation reaching bedrock [1,24,46]. In 2009, 2010, and 2012 fieldwork at Shelter B was carried out aiming at enhancing the stratigraphic and chronological resolution achieved by Wijeyapala in the 1980s, and to excavate the lower portions of the deposit to bedrock [24]. The most recent excavations were undertaken in a 300cm × 100cm × 220cm trench positioned in the east-west direction of the southern profile of 1986 excavation (Fig 2).

Stratigraphy and chronology

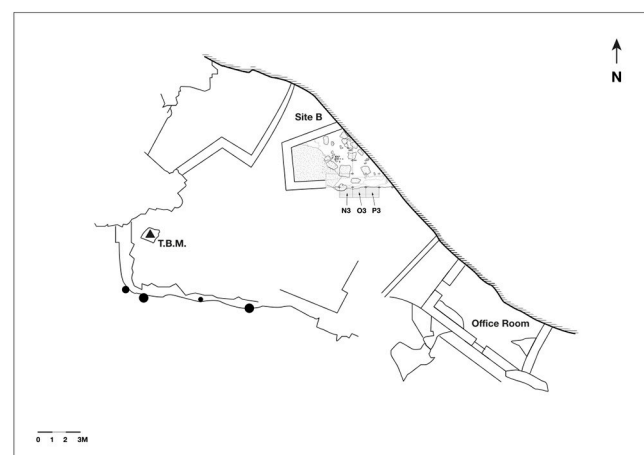
The stratigraphic and chronological analysis of Fa-Hien Lena has been developed by Wijeyapala [24], Kennedy [27], and Wedage et al. [26] over the course of the last three decades. The sediment fill of Fa-Hien Lena Shelter B consists of c. 170cm of stratified detrital sediments deposited on the heavily weathered and phantomed gneiss bedrock (Fig 3). Based on recent re-dating efforts, these deposits date from as early as c. 48,000–45,000 cal. years BP [26]. The fossils found at Fa-Hien Lena [1,24,27], and their associated material culture, thus represent the earliest definitive evidence for *H. sapiens* in Sri Lanka and South Asia more broadly. Radiocarbon dates cluster into four distinct age ranges, separating the stratigraphy into four distinct phases, each correlating with a major period of human occupation of the cave (Fig 3) (Table 2) [26].

Phase D (Late Pleistocene) deposits begin with pebbly clayey loams with angular gneiss spalls, followed by sub-horizontal layers of dark, sandy silt and laminated ash deposits inter-layered with at least two distinct accumulations of angular gneiss blocks. Faunal remains (28.7% of which are burned/calcined) and artefacts (shell beads, ochre fragments, bone points, quartz flakes) are abundant throughout. Micromorphological analysis revealed various coarse-grained microfacies (laminated and phosphatised ash intercalated with gneiss pebbles; structureless pebbly ash; microaggregated organic loam; imbricated microbreccia with charred organic matrix), all containing plentiful, well-preserved human occupation debris (charcoal, burned shell and bone, palm and many other phytoliths, quartz microflakes probably derived from lithic knapping) [26]. Phase D sediments record intermittent/episodic human occupation, from c. 48,000 to 34,000 cal. years BP, and colluvial inwash during a period of structural instability of the cave walls and ceiling. Human-mediated sediment inputs came from hearths—some *in situ*—and the cooking and consumption and discard of food remains (including the nuts of a prominent tropical and sub-tropical tree species *Canarium* sp., other, as yet unidentified plant remains, snails adapted to rainforest environments, monkeys and other predominantly arboreal mammals [26], and, possibly, the use of palm fronds for the construction of artefacts, e.g. mats, baskets and other, similar containers, as inferred from other Pleistocene sites in Sri Lanka e.g. Batadomba-lena [25]).

Fa-Hien Cave Contour Plan and Cross Section of the Fa-Hien Cave



Site B – Ground Plan



Site B – Excavation Site 2012

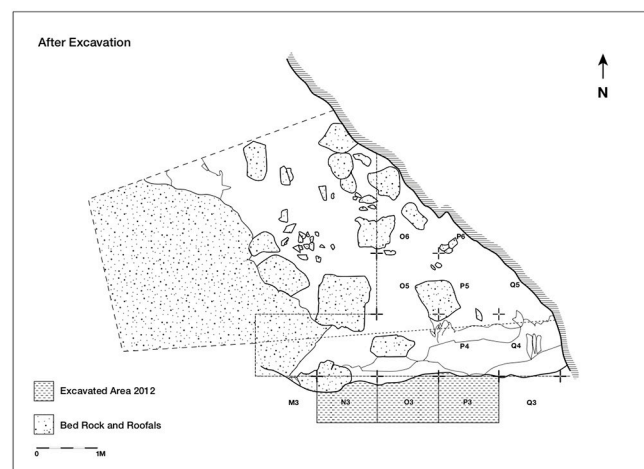
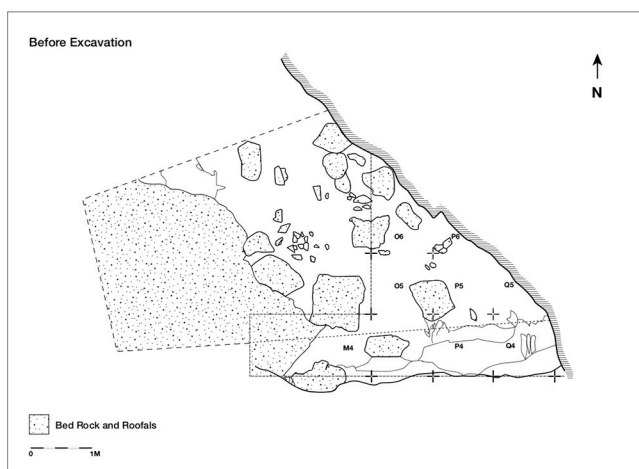


Fig 2. Fa-Hien Lena site plan. A) Elevation map of Fa-Hien Lena and surroundings. Levels based on T.B.M -200m; B) Section plan of Fa-Hien Lena; C) Ground plan of site B; D -E) Ground plan of the excavated area in 2009 and 2012.

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Phase C (Terminal Pleistocene) layers dip towards the cave wall—a pit was cut into these layers, and its fill is thus part of this phase. The deposits are heterogeneous mixtures of dark, organic-rich sandy loams and unconsolidated matrix-supported breccia with abundant charcoal and ash, either mixed with detrital sediment or present as distinct laminae/lenses.

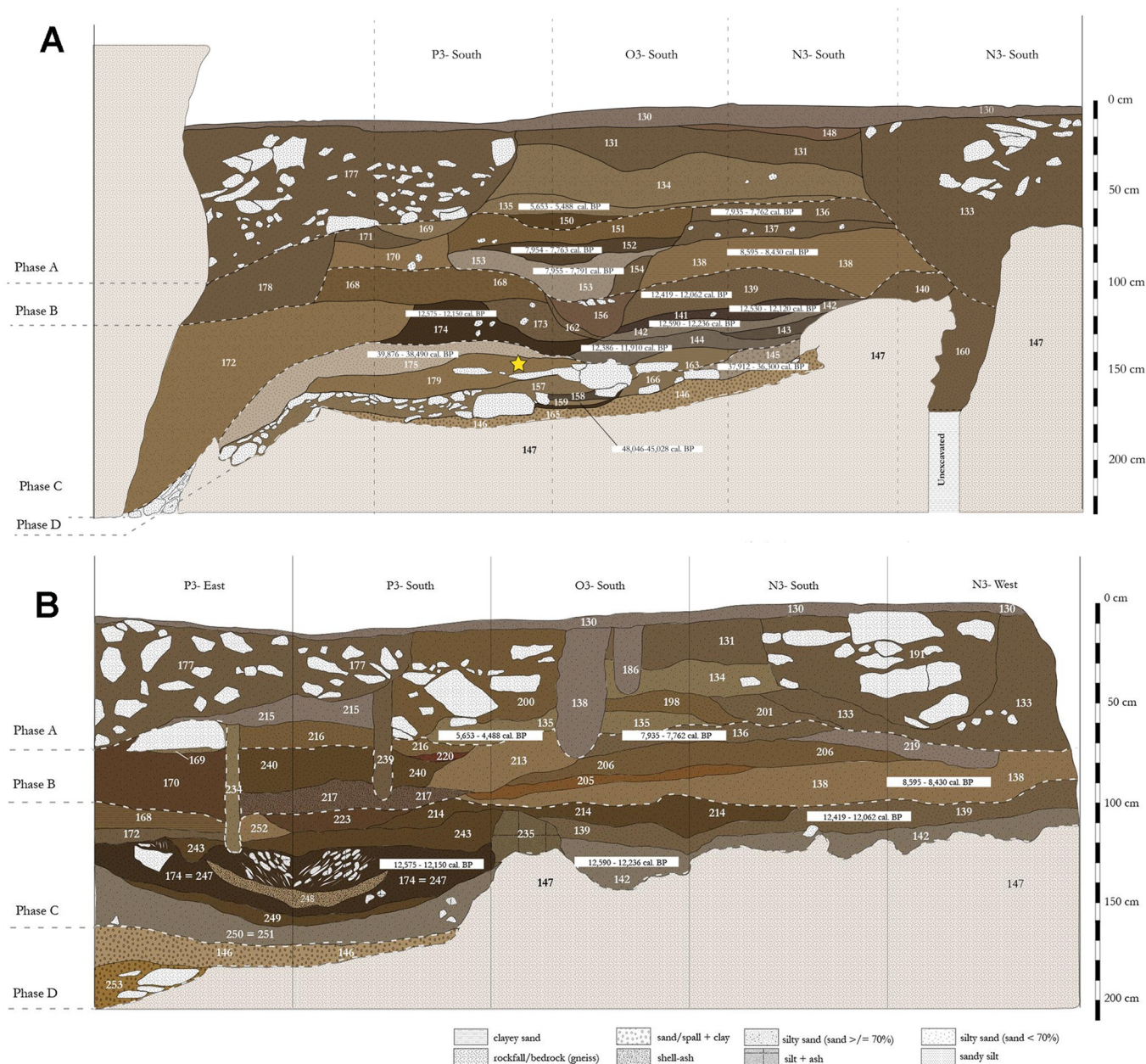


Fig 3. Fa-Hien Lena site stratigraphy. A) South wall end of the 2010 excavation taken from Wedage et al. [26]; B) South wall end of the 2012 excavation. Colours represent Munsell colour values of sediments. Phases D, C, B, and A, and their associated radiocarbon age brackets (see also [26]). Yellow star shows human fossil identified by Kennedy [27], see also Wedage et al. [26].

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Table 2. Calibrated radiocarbon dates for Fa-Hien Lena published in Wedage et al. [26]. All samples have been calibrated using the OxCal 4.3 software and IntCal13 calibration curve [67–69]. *Sample rejected, see [26] for further details.

Phase	Context	Sample	Calibrated (cal. years BP)	Uncalibrated dates (years BP)
A	107	BYP2010/CX NE/N-4, O-4, 107	4,422–4,248	3,870 ± 30
	2	B-N5-2	5,594–5,322	4,750 ± 60
	31/32/135	135	5,653–5,488	4,820 ± 30
	116	BYP 2010 CX NE/O-6, 0–6, 116 middle	5,710–5,482	4,800 ± 40
B	3	B-M6-2	7,916–7,570	6,850 ± 80
	136	136	7,935–7,762	6,970 ± 30
	51/152	152	7,954–7,763	6,990 ± 40
	52/153	153	7,955–7,791	6,900 ± 40
	3a	B-N6-2a	8,020–7,794	7,100 ± 60
	51/152	152	8,180–8,020	7,240 ± 40
	138	138	8,595–8,430	7,720 ± 40
C	109	BYP2010/CX NE/N-4, O-4, 109	12,096–11,768	10,150 ± 40
	119	BYP 2010 CX NE/O-4, P-4, 119	12,380–11,844	10,250 ± 40
	144/161/164	144	12,386–11,910	10,290 ± 40
	139/140	139	12,419–12,062	10,350 ± 40
	141	141	12,530–12,120	10,340 ± 40
	237	237	12,549–12,131	10,390 ± 40
	174/246	174	12,575–12,150	10,440 ± 40
	142	142	12,590–12,236	10,430 ± 40
D	4	B-M7-3	29,126–27,872*	24,470 ± 290
	4	B-N7-3	34,656–33,686	30,060 ± 290
	118	BYP 2010 NE/O-4, 118	36,136–35,191	31,750 ± 190
	4a	B-M7-5	37,912–34,764	32,060 ± 630
	145	145	37,912–36,300	32,890 ± 240
	5	B-M6-6	38,826–35,828	33,070 ± 630
	108	BYP 2010 CX NE/O-4, P-4, 108	38,333–36,690	33,220 ± 240
	175	175	39,876–38,490	34,600 ± 320
	110	BYP2010/CX NE/N-4, O-4, 110	42,036–40,980	36,910 ± 300
	126	BYP 2010 CX NE/ O-4, 126F	42,228–41,258	37,230 ± 310
	159	159	48,046–45,028	43,000 ± 720

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Notwithstanding its apparently short chronological range (13,000 to 12,000 cal. BP), Phase C contains the densest concentration of artefacts and human occupation debris in the Fa-Hien stratigraphy. Micromorphological analysis of basal Phase C deposits shows a very sharp-based accumulation of closely packed and imbricated wood charcoal and other charred biogenic particles (bone, snail shell, other plant remains [26]) in a matrix of fine grained charred organic debris, possibly a floor wash lag or a dump/rake out deposit. Overall, Phase C deposits probably resulted from a succession of erosion, colluviation and, perhaps, dumping episodes.

Phase B (early Holocene 8,700–8,000 cal. BP) deposits come above a sharp boundary that truncates the Terminal Pleistocene layers. Phase B comprises subhorizontal layers of light brown sandy silts, unconsolidated matrix-supported collapse breccia and ash accumulations, with a moderate amount of artefacts and habitation debris, interpreted as occupation deposits and floor wash colluvia. A large (diameter: 85cm, depth: 80cm), multi-stage pit was cut into the latter. This was filled with multiple layers of sandy silt, which may have resulted from colluviation, and ash and charcoal (much of this consists of burnt *Canarium* sp. seeds), possibly due to deliberate ash dumping [26]. Phase A (mid Holocene 6,000–4,000 cal. BP) begins with

brown sandy loams and lenses of *Canarium* sp. seed charcoal (5,900 cal. BP), deposited directly above the Phase B pit and interpreted as *in situ* hearth deposits (probably from several burning episodes at the same spot), followed by colluvial deposition on the cave floor [26]. Above these come sharp-based, brown sandy and silty clays with little internal structure, interpreted as dumps, derived from prehistoric habitation contexts (c. 6,000 to 4,000 cal. BP). Brown sandy silts with gneiss spalls above Phase A (and immediately under the present cave floor) resulted from the recent extensive mining of the cave for fertiliser, and from ongoing colluviation [26].

Fa-Hien Lena Cave contains a large abundance and variety of organic materials. Monkeys and tree squirrels overwhelmingly dominate the faunal assemblage in all phases of site occupation, accounting for more than 70% of the identified remains [26]. Bone fragments with anthropogenic modification, ranging from burning to butchery marks, were recovered in all phases of site occupation. The assemblage also contains the earliest reported bone tool assemblage in South and Southeast Asia, and also one of the earliest beyond Africa [26]. Bone tools are found in all phases of site occupation [26]. The molluscan assemblage at Fa-Hien Cave is suggestive of a similar range and distribution of both freshwater and arboreal/terrestrial taxa occurring in all phases of site occupation, many taxa of which do not naturally occur in cave settings implying anthropogenic transport [26]. Furthermore, there is evidence for anthropogenic shell modification for aesthetic/ornamental purposes throughout the Late Pleistocene to mid-Holocene contexts. Utilised hematite and ochre are recorded in the all phases of the site and all phases of the site contain preserved remains of *Canarium* nuts and wild breadfruit [26].

Materials and methods

The authors declare that the entire dataset is included within the Tables, Figures, and Supporting Information (S1 Table, S1–S3 Figs) included with this manuscript. The lithic material is located in the Department of Archaeology, Government of Sri Lanka, Colombo, Sri Lanka, in a permanent repository. While there are not specific accession numbers for each artefact, artefacts are stored under the site code ‘FH’ with clear contextual designators correlating to the phasing described here. All of the data reported in the paper are presented in the main text and Supporting Information.

The purpose of this study was to understand the nature and timing of technological behaviour in lithic assemblages from the Late Pleistocene to Holocene in Sri Lanka. Previous studies and reviews of Late Pleistocene/Holocene lithic materials from Sri Lanka document the discovery of microlithic tools [1,25,33,70], yet detailed analysis has been limited to a single study undertaken at Batadomba-lena, enabling comparisons with microlithic assemblages in India and South Africa [33]. A basic description of lithic material at Fa-Hien Lena was published in Wedage et al. [26] Supplementary Note 3 but, to date, no detailed systematic analysis of lithic production strategies, forms, and materials has been available. Here, we focus on the production processes, as well as raw materials and metrics, of Sri Lankan microliths and their *débitage*, from Late Pleistocene and Holocene contexts, thereby bringing them in line with descriptions of similar toolkits in other parts of the world [71–74]. All relevant analytical permits were obtained from the Department of Archaeology, Government of Sri Lanka for the work.

We employed a *chaîne opératoire* approach to investigate lithic reduction trajectories from stone tool assemblages recovered from Fa-Hien Lena Phases D to A, including all products and by-products of reduction. This approach employs a methodological framework that defines the reconstruction of the various processes of flake production—from the procurement of raw materials, through the phases of manufacture and utilization, to final discard [75–76]. Artefacts in each assemblage were split between raw material units (RMUs), defined according

to stone macroscopic features including type of cortex, colour, grain size and texture [77]. Five basic categories of artefact were then identified: cores, flakes, chips (<10mm), retouched tools, and hammers. All cores and flakes were identified as either complete (Flake, Core) or broken (Flake Fragment, Core Fragment). The presence of cortex was recorded on all cores, flakes, and retouched tools, split into three categories of >50% cortex (referred to in the text as cortical), <50% cortex (referred to in the text as semi-cortical), and no cortex. Higher proportions of cortex remaining on an artefact are used to infer earlier stages of a reduction sequence.

Preliminary study [26] indicated the presence of a number of distinct artefact forms that we describe below and in Table 3. Two distinct reduction methods have been identified: freehand percussion and the bipolar knapping technique. Freehand percussion involves holding a core in the hand and striking it with a hammer to remove flakes, whereas in bipolar reduction, the core is held against an anvil when struck. The force applied from the hammerstone produces two opposed impact points: one on the upper face of the core and the second on the lower face that is in contact with the anvil. Since in this percussion technique (bipolar knapping *sensu stricto*) the core is perpendicular to the anvil, flakes are produced by the hitting of the hammerstone with the upper face and by the counterstrikes of the core with the anvil. During the analysis, the variant proposed by Hiscock [78] (bipolar-rested) has also been taken into consideration, in which the core morphology could change during the reduction and flakes could be produced without requiring two aligned opposing impact points. Generally, the morphology of the raw material determines how the pebble is placed on the anvil.

We have discriminated between the vertical axial knapping, when the pebble is oriented along the longer axis, and horizontal axial knapping, when the pebble is oriented along its shorter axis. During bipolar knapping, the striking angle tends to be ~90°, although some variations could be produced by fractures, changing of the striking platforms, or re-organization of the core volume []. The striking of the hammerstone on the upper face of the core may produce battering marks, Hertzian cone and linear striking platforms complemented by scaled or invasive bifacial detachments, or a pointed striking platform [79–82]. Analyses of bipolar reduction sequences were undertaken following more recent definitions based on experimental knapping data [79–82]. The bipolar technique differs from freehand knapping in terms of:

Table 3. Descriptions of key artefact types used in the analysis of lithic assemblages from Fa-Hien Lena.

Type	Description	References
Bipolar Core	Held against an anvil when struck with a hammer, bipolar cores often display two opposed and often crushed platforms for a single negative scar, yielding two distinct initiation points	[79–86]
Freehand Core	Held in the hand when struck, freehand cores exhibit a single initiation point for each negative scar	[79–86]
Core on Flake	A core produced on a flake (i.e. presenting a clear ventral surface) where negative scars appear targeted to remove flakes rather than impose shape	[79–86]
Microlith	Small flakes with a percussion axis length of less than 40mm that are targeted products of a reduction sequence	[44]
Bladelet	Elongate flakes (i.e., length:width >2:1), wider than they are thick, with less than 20% dorsal cortex, and exhibiting one or more dorsal ridges running roughly parallel to the percussion axis, with a percussion axis length of less than 40mm	[44]
Backed Microlith	Flakes or bladelets, with a percussion axis length of less than 40mm, whose lateral margins (usually one but sometimes two or more) have been partially or completely steeply retouched by using either bidirectional flaking or very steep and often stepped dorsal retouch	[44]
Bipolar Spall/ <i>bâtonnet</i>	Non-cortical flakes with longitudinal fractures and triangular/quadrangular sections	[87]
Splinter Flake	Splintered piece with more or less pronounced traces of longitudinal fracture	[87]

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a) fracture mechanics—the former includes wedging initiations, compression–propagation and preferential axial terminations; and, b) direction of the detachments—freehand reduction is often secant to one of the core axes and, when it is parallel, it requires the preparation of a striking platform [79–82]. Examination of core and flake scar patterning (e.g. unidirectional, bidirectional, orthogonal [perpendicular], radial) is used to infer patterns of core rotation [83–85].

The identification of the byproducts of bipolar percussion is not an easy task and it has been a matter of debate for decades [79–85]. The main issue is that the knapper has poor control over blanks produced, and flakes and fragments (e.g. basal, parasitic or irregular) could be detached from surfaces not involved in the knapping reduction. Generally, bipolar flakes show different morphologies and sizes, with diffuse bulbs of percussion, shattered platforms, and opposed fracture edges (e.g. hinge, step).

The use of excessive force while knapping or the presence of an irregular structure in a raw material can result in the production of flakes that are fragmented at the point of removal, rather than through their subsequent use or taphonomic impacts. In this investigation, flake fragments were differentiated following the criteria of Mourre [86]: a) *siret sensu strico* (x1) is considered a fracture parallel to the flaking axis that divides the blank in two parts, more or less equal; b) *siret sensu lato* (x2) is considered a fracture that removes a portion of the flake's proximal side secant to the direction of the flaking axis; c) *siret sensu lato* (x3) is considered a fracture that removes two opposed portions of the flake's proximal side obliquely to the direction of the flaking axis. Often, the remaining part of the platform shows a pointed morphology. Siret fractured flakes are typical byproducts of bipolar knapping strategies, though they may also be produced by freehand reduction methods. Backing, the use of steep or blunting retouch typically applied to the dorsal face of a flake, is a distinctive retouching strategy that is readily used to classify backed artefacts. The definition of microliths and microblades is more subjective. Here, we employ a 40mm cutoff to differentiate small from large flakes and blades, following the work by Petraglia and colleagues in southern India [44].

The maximum dimension and weights of all artefacts were recorded to evaluate metric characteristics of the lithic assemblages and enable assessment of targeted blank sizes, the impact of reduction intensity on flaking sequences, and discard thresholds. Statistical analysis of significant differences in maximum dimension and weight of cores and complete flakes was conducted using the free software PAST [88]. Preliminary testing using the Shapiro-Wilk test identified non-normal distributions of these data, resulting in the application of non-parametric tests (Mann Whitney test, $\alpha = 0.05$) to examine differences in average artefact weight and maximum dimension between different raw materials and for cortical and non-cortical artefacts in each assemblage where $n > 20$ (comparable to methods in Lewis [32]). Below this threshold descriptive statistics are used for comparisons. In order to compare the distribution of the length and weight of the cores, the data were firstly transformed to log10 values and then plotted in a scatterplot.

Results

Lithic analysis by Phase

The lithic assemblage of Fa-Hien Lena Cave is comprised of 9,216 artefacts distributed across four occupation phases (Table 4, S1 Table). The dominant raw material used at Fa-Hien Lena is quartz. River pebbles with smooth, cortical external surfaces were most likely gathered from the stream located 200m from the site (Fig 2). Macroscopic analysis permitted evaluation of the quality of quartz, ranging from higher quality varieties of automorphic quartz (crystal or hyaline, milky and rose) and poorer grade types of xenomorphic quartz (vein and grainy). A

Table 4. Total number of lithic artefacts by chronological phases at Fa-Hien Lena Cave.

Layer	Flake	Bladelet	Flake Fragment	Chips	Tool	Core	Core Fragment	Hammer	Total
A	351	3	787	1144		22	16		2323
%	15.1	0.1	33.9	49.2		0.9	0.7		100
B	326	6	846	1262		20	10		2470
%	13.2	0.2	34.3	51.1		0.8	0.4		100
C	243	3	773	1639		18	13	4	2693
%	9	0.1	28.7	60.9		0.7	0.5	0.1	100
D	290	13	659	743	3	9	9	4	1730
%	16.8	0.8	38.1	42.9	0.2	0.5	0.5	0.2	100
Total	1210	25	3065	4788	3	69	48	8	9216
%	13.1	0.3	33.3	52	0.03	0.7	0.5	0.07	100

<https://doi.org/10.1371/journal.pone.0222606.t004>

few chert flakes were also recognised, although there is no known source for this material within a 5km radius.

Phase D (48,000–34,000 cal. BP). The lithic assemblage of Phase D is composed of 1,730 artefacts (1,726 débitage byproducts and four hammerstones). The assemblage is dominated by small chips (43%) and flake fragments (38%), with complete flakes and cores occurring in smaller amounts (Tables 4 and 5). Crystal and milky quartz is the primary raw material (Table 4, Fig 4). Technological analysis of the core assemblage revealed the use of the bipolar method (Fig 5: 1, 2, 4–8). Four cores in crystal quartz were reduced along their longest axis (vertical axial). The flaking surfaces are characterised by bidirectional detachments produced by the hammerstones and contact with the anvil. In two examples, the repeated battering of the hammerstones produced bifacial detachments on the proximal sides creating platforms with conical morphologies (Fig 5: 4). The use of a freehand knapping strategy is documented in two exhausted core-on-flakes. In the first example, the ventral surface of a flake was used as the striking platform for the abrupt unidirectional production of elongated flakes (Fig 5: 3). In the second core, broken during the knapping event, two small flakes were detached from the ventral surface.

The analysis of the bipolar cores in milky quartz reveals a different approach to the knapping process. Generally, the flaking sequence started with recurrent detachments along the

Table 5. Counts, mean (μ) and standard deviation (σ) of the metric attribute (mm) of the cores in crystal and milky quartz of Fa-Hien Lena Cave.

Phase	Attributes	Crystal quartz			Milky quartz		
		N°	μ	σ	N°	μ	σ
A	Length	6	23.7	9.2	14	28.4	8.04
	Width		18.7	5.2		28.5	11.2
	Thickness		13.4	4.7		18.9	7.05
B	Length	8	21.9	5.4	12	35.2	14.3
	Width		21.9	5.3		30.9	12.9
	Thickness		15.6	6.6		21.1	6.5
C	Length	7	23.5	10.9	10	29.8	6.03
	Width		16.9	8.5		24.8	8.9
	Thickness		12.4	5.2		17.5	6.9
D	Length	5	26.4	4.3	4	30.8	5.2
	Width		22.2	4.6		25.6	4.05
	Thickness		14.6	2.6		21.7	2.3

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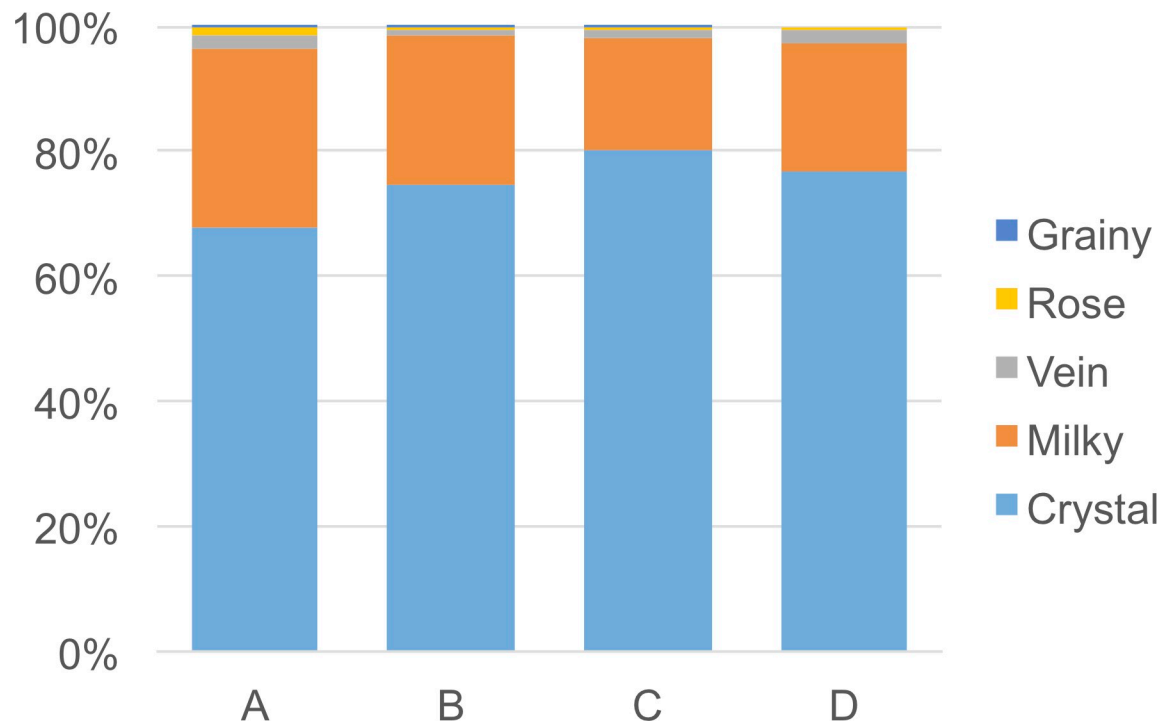


Fig 4. Frequency of quartz types by chronological phases recorded at Fa-Hien Lena Cave.

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longest axis, yielding by-products with rectilinear or convex edges. One core was discarded after having been fractured at the distal end. The remaining three cores at some point were rotated by 90° and a new production on the shorter side (horizontal axial) was initiated (Fig 5: 1, 2). Rotation of the cores, with simultaneous changes of the striking platforms, is documented several times and, most likely, was performed in order to facilitate a more secure placing of the core on the anvil as the morphology of the pebble changed during the knapping process. This technical expediency produced orthogonal scars on the ventral surfaces of the cores. Measurement of the size of the scar negatives indicated that the produced blanks would have been small, generally shorter than 20mm.

A comparison of the descriptive statistics suggests comparable average lengths and widths for crystal and milky quartz cores, but the milky quartz cores are notably thicker on average (Table 5). The higher quality of the crystal quartz probably allowed for better exploitation of the pebbles, whereas milky quartz cores were reduced less intensely. This result is also supported by the higher frequency of crystal quartz complete flakes in comparison with the other types of quartz (Table 6).

The analysis of the crystal and milky quartz flake assemblages indicates that primary decoration and tool production occurred on site, including the presence of core edge flakes that may have helped to manage flaking surfaces (Table 6, Fig 6). Conversely, artefacts in vein and rose quartz are very few and mostly associated with the early stages of reduction (Table 6). The data on the crystal quartz reveals higher frequencies of cortical blanks and unbroken flakes and bladelets (Table 6). No clear evidence for the application of a dedicated laminar reduction approach is evident, suggesting that these bladelets were the product of bipolar reduction. Although the rotation of the cores is documented only in milky quartz, orthogonal scars were found in eleven flakes of crystal quartz (Fig 6: 7) and in two flakes of milky quartz (Fig 6: 3, 8). The statistical comparison between the dimensions of unbroken blanks indicates a significant



Fig 5. Cores of Phase D and C: bipolar core (no. 4, 5, 6), bipolar orthogonal core (no. 1, 2, 7, 8), unidirectional abrupt core (no. 3).

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difference between the average length value of cortical ($n = 42$) and non-cortical ($n = 205$) flakes in crystal quartz (Mann Whitney $p = 0.0012$). Descriptive statistics suggest no

Table 6. Total number and percentage of lithic artefacts in Phase D.

	Crystal	%	Milky	%	Vein	%	Rose	%	Total	%
Cortical flake >50%	11	0.8	5	1.4	1	3.1			17	1
Cortical flake <50%	29	2.2	11	3.1	3	9.4	2	16.7	45	2.6
Cortical core-edge flake	2	0.2							2	0.1
Flake	175	13.2	27	7.6	5	15.6			207	12
Splinter flake	16	1.2	1	0.3					17	1
Core-edge flake	1	0.1	1	0.3					2	0.1
Bladelet	13	1							13	0.8
Bâtonnet	6	0.5	1	0.3					7	0.4
Cortical flake fragment	34	2.6	16	4.5	2	6.3	5	41.7	57	3.3
Siret x1	9	0.7	4	1.1					13	0.8
Siret x2	4	0.3							4	0.2
Siret x3	4	0.3	1	0.3	1	3.1	1	8.3	7	0.4
Flake fragment	320	24.1	92	26	11	34.4	3	25	426	24.7
Siret x1	53	4	14	4	2	6.3			69	4
Siret x2	35	2.6	6	1.7					41	2.4
Siret x3	31	2.3	4	1.1					35	2
Chips	574	43.2	163	46	6	18.8			743	43
Microlith	3	0.2							3	0.2
Core	5	0.4	4	1.1					9	0.5
Core fragment	3	0.2	4	1.1	1	3.1	1	8.3	9	0.5
Total	1328	100	354	100	32	100	12	100	1726	100

<https://doi.org/10.1371/journal.pone.0222606.t006>

substantive difference between cortical (n = 16) and non-cortical (n = 29) flakes in milky quartz (Tables 7 and 8).

Typical by-products of bipolar reduction, including *bâtonnet* flakes and splinter flakes [44,89], are present in the assemblage (Table 6). Splinter flakes could be produced at any stage of the knapping process and were identified in seven semi-cortical flakes of crystal quartz and one semi-cortical flake of milky quartz (Fig 6: 4). Since quartz is not a homogeneous raw material, the presence of internal flaws and crystalline surfaces could cause unintentional breakages during knapping events [90]. Due to the crystallographic features of the quartz pebbles, a high percentage of fragments are recorded within the assemblage. Within this category, siret fractures *sensu stricto* are common (Fig 6: 2) whereas siret breakages *sensu lato* are recognised in lesser frequencies (Table 6).

Retouched tools occur in the form of three microliths in crystal quartz (Fig 7): a) a crescent microlith with a continuous backed retouch along one side and two notch fractures on the cutting edge found in layer 165; b) a laminar microlith fragment with a bend fracture and a backed retouch on both edges found in layer 158; and, c) a laminar microlith with a step terminating breakage and a backed retouch on both edges found in layer 175. Ongoing functional study of these artefacts by Dr. Michelle Langley, Griffith University, Brisbane, Australia is examining whether the breaks that have been identified relate to their use (e.g. as impact fractures).

Phase C (13,000–12,000 cal. BP). The lithic assemblage of Phase C comprises 2,693 artefacts (2,689 lithic items and four hammerstones) (Tables 4 and 9). Small chips and flake fragments account for 89.6% of the lithic materials whereas complete flakes and cores are recorded in a much smaller number (Table 6). Crystal and milky quartz are the most commonly used raw materials followed by vein, rose, and grainy quartz (Table 9, Fig 4). The diacritic reading of the scars on cores and flakes allowed for the identification of the use of bipolar knapping on

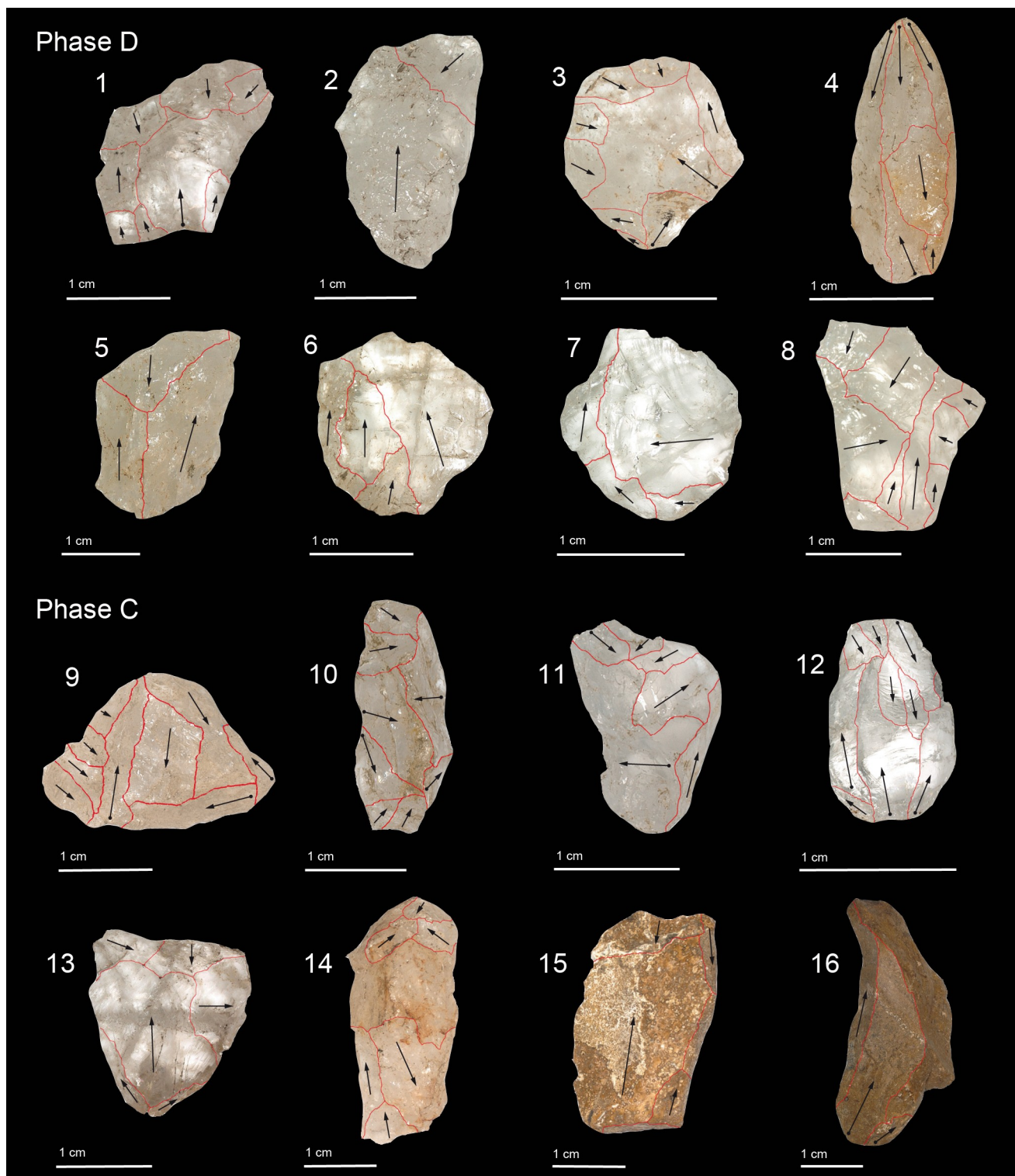


Fig 6. Flakes of Phase D and C: bipolar flake (no. 1, 5, 6, 14), bipolar orthogonal flake (no. 3, 7, 8, 9, 11, 13), splinter flake (no. 4, 10, 12), bipolar flake with sirtet sensu stricto fracture (no. 2), unidirectional flake fragment on chert (no. 15), semi-cortical flake on chert (no. 16).

<https://doi.org/10.1371/journal.pone.0222606.g006>

Table 7. Count, mean (μ) and standard deviation (σ) of the length (mm) of cortical flakes in Fa-Hien Lena Cave.

Phase	Crystal			Milky			Vein			Rose			Grainy			Chert	
	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ
A	60	18.3	6.2	57	21.4	7.3	4	20.2	10.1	6	19.4	3.9	2	42.5	15.3		
B	47	18.9	5.9	47	22.4	10.5	5	22.2	2.8	3	29.4	2.5	1	70.7			
C	44	19.2	7.2	22	21.6	8.4	2	17.8	1.5	5	25.8	8.1				1	58.1
D	42	20	7.01	16	22.5	6.8	4	19.5	3.7	2	12.8	2.5					

<https://doi.org/10.1371/journal.pone.0222606.t007>

the anvil (Fig 5: 5–8). Cores in crystal quartz are small and generally exploited along their longest axis for short knapping sequences. In one pebble, the reduction was horizontal axial and the core was discarded after a short knapping sequence (Fig 5: 5). The negative scars on previous detachments are small and less than 15mm. Only one artefact shows rotation of the striking platform from a vertical to horizontal reduction (Fig 5: 8). This latter core is also covered in red ochre.

In milky quartz, seven cores are exploited vertically but, in some of them, internal flaws caused unexpected breakages during knapping. In two artefacts, the battering of the hammerstone caused a longitudinal fracture, removing distal portions of the core (Fig 5: 6). In another, the blows on the anvil provoked the fracture of the distal margin. A fifth core was discarded because impurities in the quartz pebble caused detachment of two large portions of the flaking surface and created a step on the mesial side. Horizontal reduction of the flaking surface is documented in four of the remaining cores (Fig 5: 7). These cores are small, and their rotation could be interpreted as technical expediency to exploit the raw material more efficiently. A rose quartz core was also discovered in the assemblage (22.2 x 26.6 x 16.2mm). This artefact is small with a pronounced Hertzian cone on the proximal side. The flaking surface shows bidirectional negative scars and a fracture on the distal margin. In contrast to Phase D, average descriptive statistics suggest no notable differences in core sizes in Phase C (Table 5).

In the flake assemblage complete technological sequences are documented in crystal and milky quartz, whereas in the other quartz types only a few flakes were produced during phases of decortication (Table 9, Fig 6). Most of the cores retain cortical portions on their surfaces. The recovery of several cortical flakes supports the hypothesis that knapping activities were carried out at the site. A significant statistical difference is recorded between the average length value of unbroken cortical ($n = 44$) and non-cortical ($n = 142$) flakes in crystal quartz (Mann Whitney $p = 0.0002$), whereas no difference is documented between cortical ($n = 22$) and non-cortical ($n = 25$) flakes in milky quartz (Mann Whitney $p = 0.4620$) (Tables 7 and 8).

The data suggests that quartz pebbles were of low quality, since most the lithic items broke during knapping events (Table 9). Within fragments, silet fracture *sensu stricto* are common (3.6%), while silet fracture *sensu latu* are recorded in lesser frequencies (Table 9). Splinter flakes were noted in several unbroken blanks (Fig 6: 10, 12), six semi-cortical flakes in crystal quartz, in one cortical flake, and three semi-cortical flakes in milky quartz (Table 9). A few

Table 8. Count, mean (μ) and standard deviation (σ) of the length (mm) of complete flakes and bladelets in Fa-Hien Lena Cave.

Phase	Crystal			Milky			Vein			Rose			Grainy			Chert	
	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ	σ	N°	μ
A	60	18.3	6.2	57	21.4	7.3	4	20.2	10.1	6	19.4	3.9	2	42.5	15.3		
B	47	18.9	5.9	47	22.4	10.5	5	22.2	2.8	3	29.4	2.5	1	70.7			
C	44	19.2	7.2	22	21.6	8.4	2	17.8	1.5	5	25.8	8.1				1	58.1
D	42	20	7.01	16	22.5	6.8	4	19.5	3.7	2	12.8	2.5					

<https://doi.org/10.1371/journal.pone.0222606.t008>

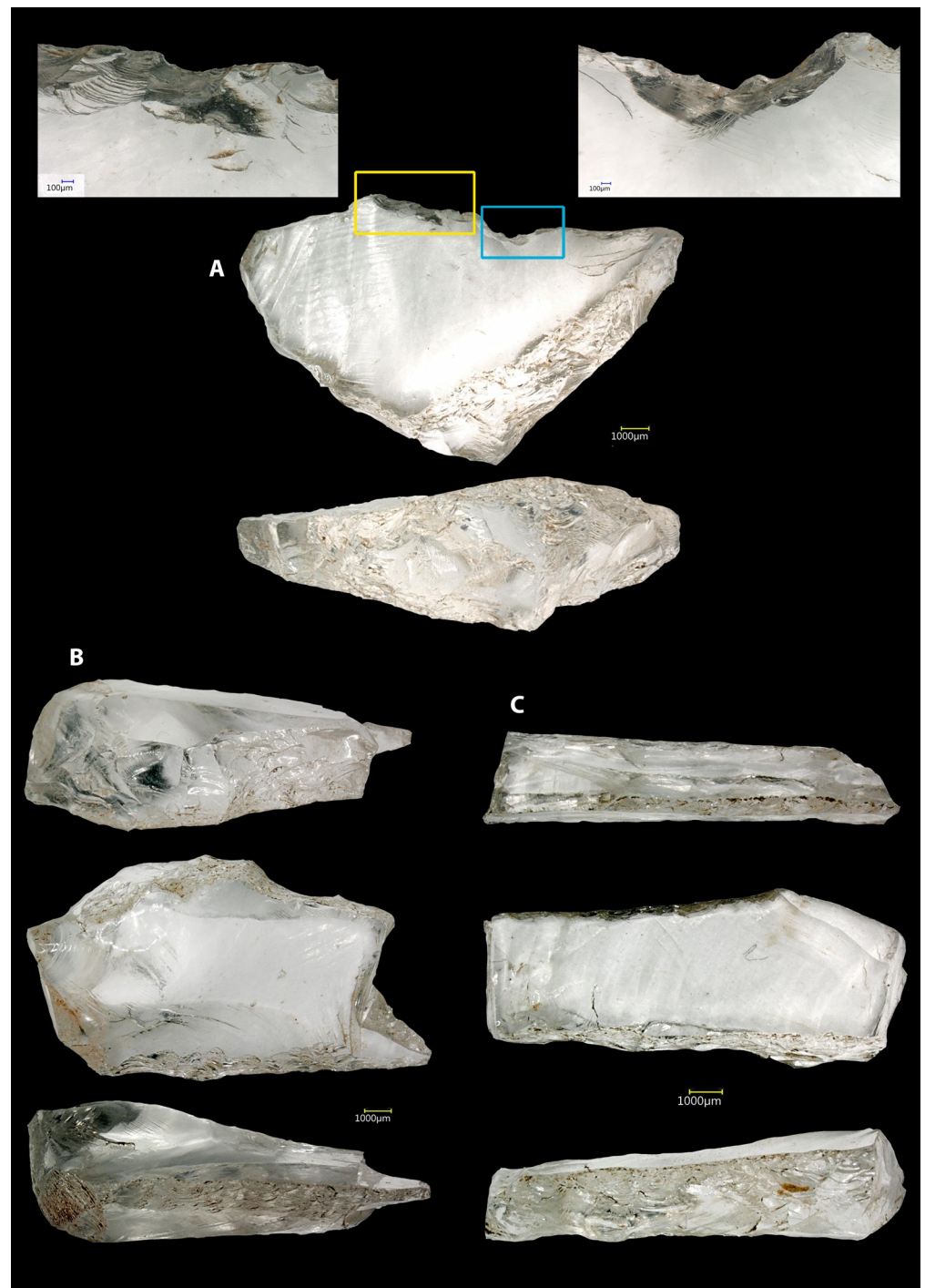


Fig 7. Microlithic tools in Phase D of Fa-Hien Lena Cave.

<https://doi.org/10.1371/journal.pone.0222606.g007>

bladelets are also present, although it appears that their production was random and not planned as in other technologies. In the complete flake assemblage, orthogonal scars on the dorsal surface attest to the rotation of the striking platform in three crystal quartz artefacts (Fig 6: 9, 11) and in one flake on milky quartz.

Table 9. Total number and percentage of lithic artefacts in Phase C.

	Crystal	%	Milky	%	Vein	%	Rose	%	Grainy	%	Chert	%	Total	%
Cortical flake >50%	6	0.3	5	1	1	3.3	3	25					15	0.6
Cortical flake <50%	33	1.5	14	2.9	1	3.3	2	16.7			1	25	51	1.9
Cortical core-edge flake	5	0.2	3	0.6									8	0.3
Flake	129	6	19	3.9	3	10					2	50	153	5.7
Splinter flake	7	0.3	5	1									12	0.4
Core-edge flake	3	0.1	1	0.2									4	0.1
Bladelet	3	0.1											3	0.1
Bâtonnet	3	0.1											3	0.1
Cortical flake fragment	45	2.1	36	7.4	6	20	1	8.3	2	28.6			90	3.3
Siret x1	7	0.3			1	3.3	2	16.7					10	0.4
Siret x2	4	0.2							1	14.3			5	0.2
Siret x3	1	0.0											1	0.0
Flake fragment	391	18.2	121	24.9	12	40	2	16.7	4	57.1	1	25	531	19.7
Siret x1	65	3	19	3.9	1	3.3							85	3.2
Siret x2	19	0.9	3	0.6									22	0.8
Siret x3	20	0.9	5	1	1	3.3							26	1
Chips	1393	64.8	241	49.7	4	13.3	1	8.3					1639	61
Core	7	0.3	10	2.1			1	8.3					18	0.7
Core fragment	10	0.5	3	0.6									13	0.5
Total	2151	100	485	100	30	100	12	100	7	100	4	100	2689	100

<https://doi.org/10.1371/journal.pone.0222606.t009>

The Phase C assemblage also included four chert artefacts: a semi-cortical flake with a cortical platform and a unidirectional negative scar on the dorsal surface (Fig 6: 16), two small unidirectional flakes (Fig 6: 15), and a proximal fragment (Table 9). These flakes were produced

Table 10. Total number and percentage of lithic artefacts in Phase B.

	Crystal	%	Milky	%	Vein	%	Rose	%	Grainy	%	Chert	%	Total	%
Cortical flake >50%	15	0.8	15	2.6	2	9.1	1	9.1	1	14.3	1	33.3	35	1.4
Cortical flake <50%	32	1.7	29	5	2	9.1	2	18.2					65	2.6
Cortical core-edge flake			3	0.5	1	4.5							4	0.2
Flake	149	8.1	43	7.4	3	13.6			2	28.6	1	33.3	198	8
Splinter flake	15	0.8	9	1.5									24	1
Bladelet	5	0.3	1	0.2									6	0.2
Bâtonnet	2	0.1											2	0.1
Cortical flake fragment	53	2.9	36	6.2	3	13.6	2	18.2					94	3.8
Siret x1	5	0.3	7	1.2	1	4.5	1	9.1					14	0.6
Siret x2	3	0.2	2	0.3									5	0.2
Siret x3	3	0.2	5	0.9									8	0.3
Flake fragment	434	23.5	144	24.7	2	9.1	3	27.3	1	14.3	1	33.3	585	23.7
Siret x1	52	2.8	34	5.8	1	4.5	1	9.1					88	3.6
Siret x2	22	1.2	6	1									28	1.1
Siret x3	17	0.9	5	0.9									22	0.9
Chips	1027	55.7	224	38.4	7	31.8	1	9.1	3	42.9			1262	51.1
Core	8	0.4	12	2.1									20	0.8
Core fragment	1	0.1	9	1.5									10	0.4
Total	1843	100	584	100	22	100	11	100	7	100	3	100	2470	100

<https://doi.org/10.1371/journal.pone.0222606.t010>

from different chert pebbles and they were introduced to the site as transported artefacts. The technological analysis of the flakes indicates that they were produced using the unidirectional method and not the bipolar method.

Phase B (8,700–8,000 cal. BP). The lithic assemblage of Phase B is composed of 2,470 items, predominantly small chips and flake fragments (85.4%) (Table 4). The raw materials used mostly are crystal and milky quartz (Table 10, Fig 4). Technological analysis of the core and flake collection reveals the use of the bipolar method (Fig 8). In three cores made from crystal quartz, the pebbles are reduced along the longest axis. In another, the fractures on the striking platform shaped the blank into a pyramidal morphology. In the other five cores, the knappers changed the striking platforms, rotating the artefact flaking axis by 90° (Fig 8: 1, 2). It is worth noting that the striking platforms of these samples are more crushed in comparison with those of the previous phases, probably due to the use of heavier hammerstones. In one core, vertical exploitation resulted in a fracture, leading to the use of a new striking platform.

In the milky quartz assemblage, eight cores were exploited using vertical reduction (Fig 8: 3) and two of them display a pronounced Hertzian cone on the proximal side, probably caused by the recurrent battering on the same area of the platform. In five cores, the internal flaws on the raw material resulted in fracture of the striking platforms. Within this group, three artefacts document recurrent production even after breakage, with cores being shaped into a pyramidal morphology where the pointed edge is the platform and the flat surface is the distal side. A total of four cores show changes in the direction of the reduction from vertical to horizontal with a rotation of the artefacts by 90° (Fig 8: 4). On one artefact, the change in the striking platforms is likely related to the more efficient exploitation of the core since, during reduction, different fractures limited the amount of raw material available. Descriptive statistics for crystal and milky quartz indicate substantial differences in size, with milky quartz cores typically larger across all three dimensions (Table 5).

In the flake assemblage (Fig 9), complete knapping sequences are recorded in crystal and milky quartz. By contrast, in the other quartz types pebble decortication is primarily documented (Table 10). Although 65% of the cores retain some cortex on their surfaces, the amount of cortical items is larger than in the assemblages from the previous Phases (Table 10). Within the group of complete flakes, only two items in crystal quartz and one blank in milky quartz show orthogonal detachments produced during the rotation of the striking platforms. Comparison between unbroken cortical ($n = 47$) and non-cortical ($n = 169$) crystal quartz flakes indicates significant difference in the average length (Mann Whitney $p = < 0.0001$), but not between cortical ($n = 47$) and non-cortical ($n = 53$) milky quartz flakes (Mann Whitney $p = 0.5297$) (Tables 7 and 8).

Bladelets and *bâtonnets* are limited in the assemblage, whereas splinter flakes are found in four semi-cortical flakes in crystal quartz (Fig 9: 4, 6), two cortical flakes in milk quartz, four semi-cortical flakes in milky quartz (Fig 9: 7), and in one semi-cortical blank in vein quartz. Broken artefacts are very common in the assemblage and silet fractures *sensu strico* are more frequent than the other types of silet *sensu lato* in cortical and non-cortical fragments. In the assemblage from Phase B, three artefacts made from chert pebbles are also documented: one cortical flake, one proximal fragment (Fig 9: 5), and one unidirectional flake (Table 10). The chert RMU's are different from those recorded in Phase C, making it difficult to assess if they were collected in the same area.

Phase A (6,000–4,000 cal. BP). The lithic assemblage of Phase A comprises 2,323 artefacts and includes mostly small chips (49.2%) and flake fragments (33.9%) (Table 4). The predominant raw materials are crystal and milky quartz, with vein, rose, and grainy quartz being less frequent (Table 11, Fig 4). Technological analysis of the core and flake assemblage points to the use of the bipolar method (Fig 8). Four cores in crystal quartz were exploited along their

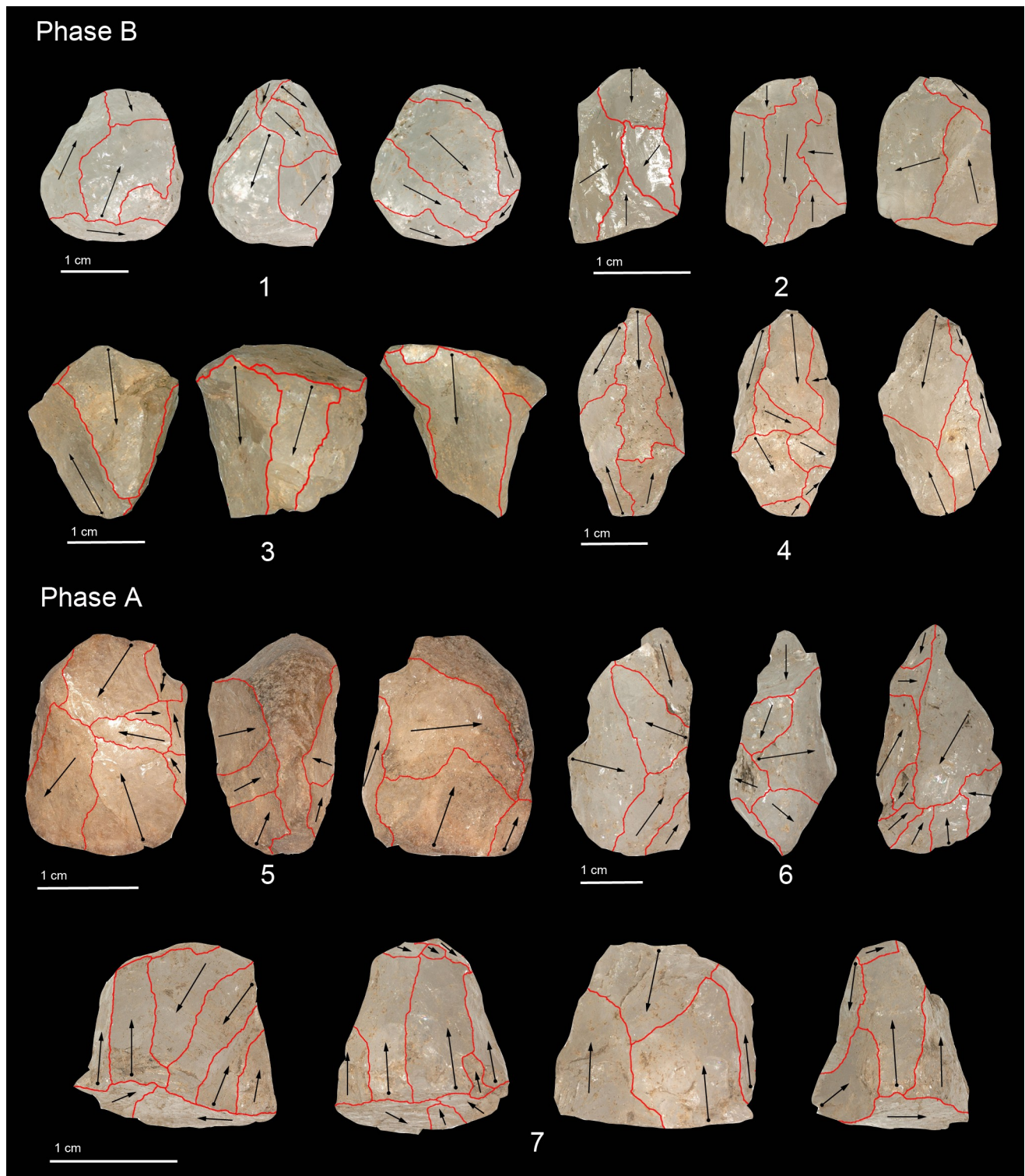


Fig 8. Cores in Phase B and A: bipolar core (3, 7), bipolar orthogonal core (1, 2, 4, 5, 6).

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longest axis and, in the case of two artefacts, internal flaws caused fracture of the striking platforms (Fig 8: 7). In addition, two other cores show that the striking platforms were rotated by



Fig 9. Flakes in Phase B and A: bipolar flake (1, 2, 3, 8, 12, 15, 16), bipolar orthogonal flake (9), splinter flake (4, 6, 7, 10, 11, 13, 14), unidirectional flake fragment in chert (5).

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90° and the lateral plain surfaces were used for short, horizontal reduction sequences (Fig 8: 5, 6).

In the milky quartz assemblage vertical reduction of the core volume is documented in eight cores, while the morphology of the pebbles favoured horizontal exploitation in two cores. In three artefacts the hammerstones broke the striking platforms, shaping the proximal surface into a conical shape. Short knapping sequences are recognised in three cores, although the pebbles retain more volume for exploitation. The change in the direction of the flaking reduction from vertical to horizontal is recorded on five cores; on two of them a fracture was used as a second striking platform. The dimensions of the core byproducts are shorter than 20mm. Despite excluding a milky quartz core weighing 457.8g as an outlier, descriptive statistics for the cores suggest milky quartz cores are notably larger than crystal quartz cores across all three dimensions (Table 5). A core in vein quartz with a cortical portion on the dorsal surface was also found in the assemblage (24.9 x 17.2 x 10.7 mm). During reduction, the core was rotated for better exploitation of the volume, producing flakes smaller than 17mm.

In the flake assemblage, different stages of core reduction, from decortication to production, are recorded in the crystal and milky quartz assemblages. By contrast to the other quartz types, most of the artefacts are associated with the cortical categories (Table 11). Comparison between the length of complete cortical ($n = 57$) and non-cortical ($n = 68$) milky quartz flakes indicates similar average values (Mann Whitney $p = 0.3203$) whereas a significant statistical difference is recorded between cortical ($n = 60$) and non-cortical ($n = 153$) crystal quartz flakes (Mann Whitney $p = 0.0006$) (Tables 7 and 8). Splinter flakes are more common in Phase A than other phases (Table 11, Fig 9: 10, 11, 13, 14). They were identified in six cortical and five semi-cortical flakes in crystal quartz, six cortical and six semi-cortical in milky quartz, one cortical and two semi-cortical flakes in rose quartz, and in one semi-cortical blank in vein quartz. The number of bladelets and *bâtonnets* is very small, while, for complete flakes, orthogonal scar negatives are documented only in one flake in crystal quartz (Fig 9: 9). Fragments are abundant in the assemblage and silet fractures *sensu stricto* are more frequent than silet fractures *sensu lato* (Table 11). Silet breakage was also identified in the single chert artefact discovered in the assemblage.

Fa-Hien Lena lithic technology through time. The Fa-Hien Lena lithic assemblage reveals remarkable long-term technological continuity in the Wet Zone rainforest of Sri Lanka, from the Late Pleistocene into the Holocene. The earliest occupation of this rainforest environment, c. 48,000–45,000 cal. years BP, is in part represented by the exploitation of local quartz pebbles using the bipolar method. Although there is a c. 20,000-year hiatus in the stratigraphic sequence between Phases D and C, the technological approaches in all phases are similar, consisting of the exploitation of the longest axis of cores and the rotation of striking platforms. Raw material provisioning was generally local: quartz pebbles were apparently collected from a nearby stream through all phases of site occupation. The diachronic comparison of raw materials indicates a uniform preference of crystal quartz, whereas a slight increase in the use of milky quartz pebbles is documented during the Early and Mid-Holocene (Fig 4). A few chert flakes of different RMUs were also recognised in the assemblage. Since sedimentary bedrock formations are not reported in the area, these chert artefacts were probably transported to the site as part of the toolkit, but the location of the chert source(s) is still unknown. Further work on raw material procurement will hopefully shed light on the mobility patterns of prehistoric foragers at Fa-Hien Lena Cave.

Quartz pebbles recovered during the excavation of the site have maximal dimensions of 50–70mm, suggesting that the starting size of raw materials selected in the nearby stream was relatively small. A core with a length of 100mm was recovered in Phase A, implying that larger nodules were occasionally available. Comparison of bipolar core metric attributes suggests that

Table 11. Total number and percentage of lithic artefacts in Phase A.

	Crystal	%	Milk	%	Vein	%	Rose	%	Grain	%	Chert	%	Total	%
Cortical flake >50%	13	0.8	23	3.5	2	4.3	2	6.3	2	50			42	1.8
Cortical flake <50%	46	2.9	34	5.1	2	4.3	4	12.5					86	3.7
Cortical core-edge flake	1	0.1											1	0.0
Flake	133	8.4	49	7.4	4	8.7							186	8
Splinter flake	16	1	18	2.7									34	1.5
Core-edge flake	2	0.1											2	0.1
Bladelet	2	0.1	1	0.2									3	0.1
Bâtonnet	3	0.2											3	0.1
Cortical flake fragment	57	3.6	77	11.6	11	23.9	9	28.1					154	6.6
Siret x1	5	0.3	13	2	1	2.2	1	3.1					20	0.9
Siret x2	4	0.3	5	0.8									9	0.4
Siret x3	5	0.3	3	0.5									8	0.3
Flake fragment	263	16.7	176	26.5	9	19.6	5	15.6	1	25			454	19.5
Siret x1	66	4.2	35	5.3	2	4.3					1	100	104	4.5
Siret x2	12	0.8	4	0.6									16	0.7
Siret x3	12	0.8	7	1.1									19	0.8
Chips	923	58.6	195	29.4	14	30.4	11	34.4	1	25			1144	49.2
Core	6	0.4	15	2.3	1	2.2							22	0.9
Core fragment	7	0.4	9	1.4									16	0.7
Total	1576	100	664	100	46	100	32	100	4	100	1	100	2323	100

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crystal cores were slightly more reduced than artefacts of milky quartz (Table 9, S1 Fig). This characteristic is also evident when assessing the mean length values of complete flakes (S2 and S3 Figs). Blanks in crystal quartz are generally smaller than artefacts in other quartz RMUs throughout the sequence (Tables 5, 7 and 8; S2 and S3 Figs). However, comparing the length and weight values reveals that cores of Phase D are more closely related than the artefacts from other phases, thereby demonstrating different degrees of reduction (Fig 10). This pattern

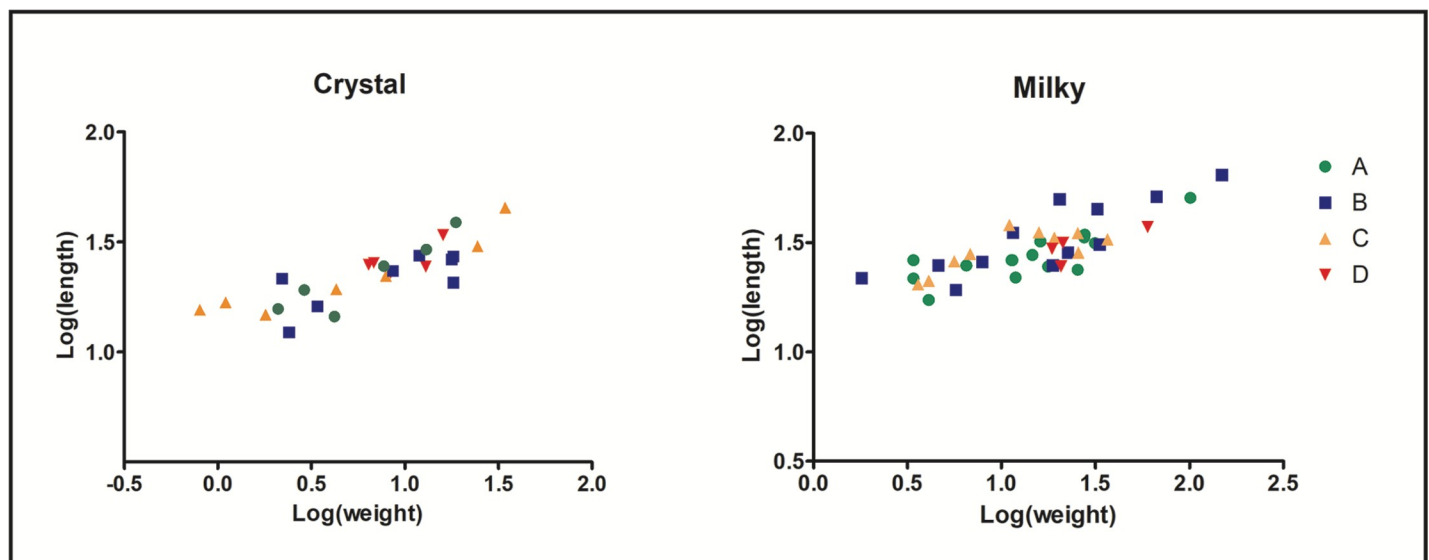


Fig 10. Log transformation plot of weight and length of cores in crystal and milky quartz of Fa-Hien Lena.

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could be explained by the decreasing quality of quartz raw materials after the earliest phases of occupation. Fractures caused by internal flaws and crystalline surfaces could have resulted in knappers discarding or exploiting pebbles in a different manner. The comparison of the length of cortical and non-cortical flakes also shows slightly larger mean values for Phase D than for the other Phases (Tables 5, 7 and 8).

Discussion

Our analysis of the Fa-Hien Lena lithics has highlighted two major properties of the assemblage: 1) high levels of technological continuity from ~48–45 ka into the Holocene, with lithic technologies focused on bipolar reduction of quartz to produce small flake blanks, and 2) the earliest appearance of backed geometric microliths in South Asia ~48–45 ka. While the number of finished backed microliths identified is low ($n = 3$) at Fa-Hien Lena, our analysis demonstrates that production is dedicated towards small flake blank manufacture below the regionally appropriate size threshold of 40mm, and thus represent microlithic technologies. Our data highlight that while backing retouch strategies were used at Fa-Hien Lena, the tools themselves may have been transported away from the site for use and discarded elsewhere. This would be in fitting with proposals that microlith tools are associated with projectile technologies during the hunting of arboreal and semi-arboreal game. However, it is also possible that backing may not always have been necessary for successful production of hafted projectiles. Although it has been suggested that the size and type of the raw material could have influenced the adoption of a particular technology [89], the recurrent application of the bipolar concept in the production of the Fa-Hien Lena lithic assemblage could be interpreted as a successful solution for coping with the daily needs for sharp tools rather than an adaptation to the quality of raw material. In Africa, *H. sapiens* practiced successful reduction of quartz nodules of small dimensions with different knapping methods from single platform to centripetal and Levallois reduction strategies [71,90–92].

The Late Pleistocene/Holocene foragers of Sri Lanka evidently used other knapping methods (e.g. freehand unidirectional reduction). The bipolar strategy could have been advantageous due to its technological flexibility, allowing a more thorough exploitation of the nodule and the production of relatively large blanks from small cores. Given the primary sourcing of raw materials from small pebbles found in local streams, such efficient reduction would have afforded a suitable supply of flakes. Furthermore, bipolar flakes/blades are generally straight and lacking pronounced bulbs, making them particularly suitable to be hafted onto wooden implements after minimal reshaping of the cutting edges [78]. Resins appropriate for hafting, such as the resin from the *Canarium* sp. trees, have been noted in ethnohistorical record of the Wanniyalaeto, the hunter-gatherer group that is now restricted to the sub-tropical forests of Sri Lanka, but which once was more widespread [1]. Below, we place these findings within their broader regional context.

Fa-Hien Lena lithic technology in regional context

Sri Lanka. Batadomba-lena provides an appropriate local comparison for the lithic technology at Fa-Hien Lena. The site, a small NE facing rockshelter, in gneiss bedrock, is located in Wet Zone lowland rainforest similar to Fa-Hien Lena [1,25,46]. It has also yielded a rich lithic assemblage from occupations commencing c. 38,000–36,000 cal. years BP. While we concentrate our discussion on qualitative comparisons of the lithic industries, it is worth noting that both sites have yielded fossil remains of *H. sapiens* that are significantly older than those from sites in India, and document specialised rainforest subsistence strategies in the form of rich organic toolkits and faunal assemblages, which are also absent until much later in other

regions of South Asia. Unlike Fa-Hien Lena, the Batadomba-lena sequence records a succession of occupations between the Late Pleistocene (Phase 7c, 36–28 ka) (i.e. after Fa-Hien Lena Phase D) to the start of the Holocene (Phase 4a, 12 ka) (contemporary with Fa-Hien Lena Phase C), with no major stratigraphic hiatus [25,70].

At both Fa-Hien Lena and Batadomba-lena, a diverse range of quartz material was exploited as the main raw material for producing small blanks. Although the use of chert is present at both sites, this material is notably absent from the oldest horizons in each sequence. Nevertheless, there are a number of differences in the stone tool technologies between these sites. At Fa-Hien Lena, lithic technology appears to be nearly exclusively based upon bipolar reduction. Although bipolar cores are the most frequent single core type at Batadomba-lena, the combined alternate types of freehand flake cores are more numerous than bipolar cores. Indeed, Lewis and colleagues [33] suggest that, based on their small size, bipolar cores represented the final phase of reduction before discard rather than independent reduction trajectories. Evidence for dedicated blade production at Batadomba-lena is preserved in two cores [33], something absent at Fa-Hien Lena. Finally, retouched artefacts are considerably more numerous in all levels of Batadomba-lena than at Fa-Hien Lena, with geometric microliths evident in all levels alongside other forms of retouched blade and flake tools.

More limited comparisons can be made with the Sri Lankan site of Kitulgala Beli-lena, another Wet Zone rockshelter where a small sample of retouched tools has been studied. At Kitulgala Beli-lena, occupation phases appear from Horizon III (31–26 ka) and continue into the Holocene, with the presence of lithic artefacts alongside organic tools and faunal assemblages [70]. Once again, the small artefact size is highlighted, with the presence of 27 geometric microliths noted from Horizon III, which then occur at lower frequency in younger levels [32,70]. Blade blanks appear to be slightly more frequent than flake blanks for retouched artefacts, although systematic study of larger sample sizes are required [32]. Late Palaeolithic industries are also apparently present beyond the Wet Zone rainforests of Sri Lanka. At the sites of Patirajawela and Bundala [1], which illustrate occupation of sand dunes close to the modern southern coastline beyond the Wet Zone, geometric microliths are reported from sediment contexts radiocarbon dated to between 28–22 ka, while thermoluminescence *terminus post quem* dates of 74–64 ka at Patirajawela remain unconfirmed [1,93].

India. The focus on bipolar technology in the earliest levels of Fa-Hien Lena, to the exclusion of other reduction strategies, stands in stark contrast to the oldest known Late Palaeolithic assemblages from India. In southern India, the oldest Late Palaeolithic assemblages come from the rockshelter site of Jwalapuram 9. This site is located at the juncture of forested uplands and a broad lowland river valley, with human occupation dating from >34 ka and persisting through the Late Pleistocene into the early Holocene [48,49]. While the earliest assemblages (Phase E) at Jwalapuram 9 indicate the use of microblade technologies, bipolar methods are absent. Although bipolar technologies only occur in low frequencies during later Phase D (~0.2%) and Phase C (~1%), microblade technologies are present throughout and become more prominent in later levels. Similarities between Jwalapuram 9 and Fa-Hien Lena can be found in the number of final retouched backed artefacts—something absent in the lowest levels but accounting for ~3.6% of the Phase D assemblage and ~4.8% of Phase C which includes backed geometric forms that typically focus on blade blanks [48]. It is notable, however, that bipolar technologies are present in late Middle Palaeolithic assemblages in the immediate vicinity at sites Jwalapuram 20, 21 and 23. At these sites bipolar technologies appear alongside blades and sparse microblades, and there is a frequent use of crystal quartz at Jwalapuram 23 [48].

The oldest Late Palaeolithic industry from central India comes from the open-air site of Mehtakheri in the Narmada valley, dating to ~45 ka [50]. Both microblade and flake reduction

sequences are recognised in this assemblage, however, as at Fa-Hien Lena the final number of retouched artefacts is small, consisting of just two backed blades [50]. Neither bipolar technologies nor geometric microliths are present, however. Further evidence for early Late Palaeolithic industries in central India comes from the open-air site of Patne, where the youngest of five assemblages (IIE) is associated with a single radiocarbon date of ~25 ka [47]. However, the site requires renewed and comprehensive dating to place the site and associated lithic assemblages in their proper context. At Patne, microlithic tools are reported from assemblages IIB onwards, alongside a range of non-microlithic retouched flake and blade tools, including backed pieces, which appear from the lowest levels of the site. A single bipolar core is reported—this is notably large (length = 51.9mm) in the context of the wider flake and blade core populations at the site [32].

In northern India, dedicated microblade technologies appear from ~55–47 ka at the site of Dhaba 3 in the Middle Son Valley, suggesting an early emergence of Late Palaeolithic industries in the region [52]. Here, Late Palaeolithic industries from open air contexts combine blade and flake reduction trajectories, while backing first appears as a retouching strategy from 42 ka and becomes more prominent by 39–26 ka. However, bipolar reduction methods are not reported from these assemblages while geometric microliths are also not clearly identifiable. The evidence from alluvial sediment sites in eastern India paints a similar picture. Microblade reduction is suggested to appear at Kana ~42 ka and Mahadebbra between ~36–25 ka, geometric backed forms are present at low frequency at Mahadebbra, while no bipolar reduction is evident at either site [53, 94]. Geometric microliths occur in low numbers at occupations of sand dune sites at Buddha Pushkar, western India, as part of a number of assemblages dating to before and after the LGM (28–16 ka) [51]. Backing appears to be a regular feature of a diverse retouched tool kit, while core reduction strategies combine blade, microblade and prepared flake core methods. A number of quartz cores from these assemblages may present evidence for bipolar reduction.

A diverse toolkit for diverse adaptations. The process of lithic miniaturisation and the production of small tools was a broad, but diverse phenomenon, appearing more prominently across many regions of Africa and Eurasia during the Late Pleistocene [36,40,41]. In South Africa, microliths appeared in several localities from c. 71 ka [95,96], whereas in East Africa backed tools only occur after 50 ka in Tanzania [97], on the coast of Kenya [11], and in Ethiopia [35,98]. Some of the earliest microlith examples, part of the Howiesons Poort techno-complex, have been argued to be short-lived phenomena [99,100]. In Europe, microliths have often been associated with the Upper Palaeolithic from c. 45 ka [61], alongside symbolic behaviour, art, and more complex hunting strategies often taken as the hallmark of the arrival of our species [101]. In the Levant, bladelet technologies and the use of backing occur from c. 40 ka, with geometric microliths appearing at sites such as Ksar Akil from ~27 ka [102]. Further east, in northern Asia, microblade technologies emerge as part of the 'Initial Upper Palaeolithic' c. 48 ka [103,104], while in Central Asia geometric microliths and backed bladelets appear as 'Upper Palaeolithic' industries from 32 ka [105]. In eastern Asia, microblade technologies emerge in China and the Korean Peninsula from ~30 ka [106,107]. In Southeast Asia, the absence of microlithic technologies until the Holocene is particularly notable [108], and broadly paralleled by the archaeological record of Australia [39] though microliths are known from Pleistocene sites in Queensland and New South Wales [109–111]. Therefore, the archaeological record of Fa-Hien Lena, where lithic technologies targeting small blank sizes and including backed geometric tools appear sometime between 48,000–45,000 cal. years BP, constitutes some of the earliest evidence for microlithic technology outside Africa.

The global emergence of microlithic technologies appears to be the result of technological convergence, rather than the result of dispersal from a single origin [39]. The diversity of

ecological contexts in which microlithic technologies appear to have been independently innovated is particularly startling. In this context, Fa-Hien Lena documents the earliest use of microlithic technologies in tropical rainforest habitats. Long-term lithic technological stability from the Late Pleistocene to the Holocene in tropical contexts is also potentially seen in South-east Asia. In the territories between Thailand, south China, Vietnam and northwest of Sumatra, the Hoabinhian techno-complex persisted from ~43 to 4 ka [107–110,112–115]. This industry is characterised by plain pebbles, with partially ground edges, choppers, chopping tools, unmodified flakes and the Sumatralith, an oval cobble unilaterally retouched, and short-axes made of transversally fractured tabular cobbles that are also unilaterally retouched [116]. Although the evidence is scarce, probably due to preservation bias, bone points were also documented in the Hoabinhian toolkit after 22 ka [22]. Similar continuity of technological strategies is also observed across island Southeast Asia, at the Niah Caves in Borneo (45–2.5 ka) [2], Jerimalai in East Timor (42–9 ka) [117], and in the Philippine Archipelago from the mid-Late Pleistocene [118].

Appearing in different forms [119], in different environments [33,39,49,70], and sometimes even out of earlier ‘Middle Palaeolithic’ industries [49], microliths are evidently not a marker of rapid expansion of *H. sapiens* beyond Africa from c. 60 ka. However, their proliferation across Eurasia between c. 48–45 ka, in a number of diverse environments, does perhaps still manifest something uniquely human. It was recently proposed that our species was ecologically unique relative to previous members of the genus *Homo*—simultaneously generalising in a diversity of environments while also specialising at the population level in the use of specific resources and landscapes [23]. The diverse temporal appearance of different microlithic forms in sub-Saharan Africa, East Africa, temperate Europe, the Mediterranean, northern and eastern Asia and, now, tropical rainforests is perhaps a material correlate of such a capacity, highlighting the adaptive plasticity of *H. sapiens* as it colonised nearly all of the world’s environments during the Late Pleistocene [23,120]. Alongside symbolic material culture [121] and evidence for increased social interaction [17,122], the technological flexibility afforded by microliths may have contributed to a contingent ability to make use of diverse animal and plant resources [123]. While they undoubtedly conferred unprecedented advantages in certain settings, microliths were just one part of what enabled our species to expand and sustain itself in the various ecosystems that have made up its range since the Late Pleistocene.

Conclusions

Here, we present the first detailed analysis of the earliest microlith assemblage in South Asia (48,000–45,000 cal. years BP), located in tropical rainforest on the island of Sri Lanka. Between c. 48–45,000 to 4,000 cal. years BP, despite a long stratigraphic hiatus, technological processes of production and raw material choices show clear continuity, implying a long-term stable adaptation in this part of the world. As old as those found in Europe (~45 ka [61]), the microlith assemblages of Sri Lanka encourage a context-specific approach to these tool types, one that is not limited to savanna, woodland, or coastal plain settings. We argue instead that the recurrent and variable development of microlith technologies is a proxy for the inherent ecological and cultural plasticity of *H. sapiens* as it inhabited a diversity of environments and continents on its expansion within and beyond Africa in the Late Pleistocene. It appears likely that, in the Sri Lankan context, microliths may have formed part of composite projectile technologies that enabled the specialised capture of semi-arboreal and arboreal prey; however, more use-wear work is required to confirm this. Technological stability seems to be a feature of tropical rainforest environments in Asia during the Late Pleistocene, potentially highlighting commonalities in the use of lithics in such settings, as well as the possible reliance on tools

made from perishable organic materials. Significantly, microliths were clearly a key part of the flexible human ‘toolkit’ that enabled our species to respond—and mediate—dynamic cultural, demographic, and environmental situations [see also 64] as it expanded over nearly all of the Earth’s continents during the Late Pleistocene, in a range currently not evident among other hominin populations.

Supporting information

S1 Table. Total number of lithic artefacts by chronological phase at Fa-Hien Lena Cave.
(DOCX)

S1 Fig. Comparison of core length and raw material for the different phases of occupation at Fa-Hien Lena Cave.
(TIFF)

S2 Fig. Comparison of complete cortical flake length and raw material for the different phases of occupation at Fa-Hien Lena Cave.
(TIFF)

S3 Fig. Comparison of complete flake length and raw material for the different phases of occupation at Fa-Hien Lena Cave.
(TIFF)

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Late Pleistocene to Early-Holocene Rainforest Foraging in Sri Lanka: Multidisciplinary analysis at Kitulgala Beli-lena[†]

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Abstract

Sri Lanka has produced the earliest clear evidence for *Homo sapiens* fossils in South Asia and research in the region has provided important insights into modern human adaptations and cultural practices during the last *ca.* 45,000 years. However, in-depth multidisciplinary analyses of Late Pleistocene and Holocene sequences remain limited to just two sites, Fa Hien-lena and Batadomba-lena. Here, we present our findings from the reinvestigation of a third site, Kitulgala Beli-lena. New chronometric dating from the site confirms the presence of humans as early as *ca.* 45,000 cal. BP. in the island's Wet Zone rainforest region. Our analyses of macrobotanical, molluscan, and vertebrate remains from the rockshelter show that this early human presence is associated with rainforest foraging. The Late Pleistocene deposits yielded evidence of wild breadfruit and kekuna nut extraction while the Holocene layers reveal a heavy reliance on semi-arboreal and arboreal small mammals as well as freshwater snails as a protein source. The lithic and osseous artefacts demonstrate that populations developed a sophisticated tool kit for the exploitation of their immediate landscapes. We place the rich Kitulgala Beli-lena dataset in its wider Sri Lankan context of Late Pleistocene foraging, as well as in wider discussions of our species' adaptation to 'extreme' environments as it moved throughout Asia.

Keywords:

Rainforest, Human adaptation, Modern human dispersal, South Asia, Pleistocene Archaeology

1. Introduction

South Asia has emerged as a crucial region for understanding the timing and nature of human dispersals from Africa and the Middle East into Southeast Asia and Australasia (Petraglia et al., 2012; Blinkhorn et al., 2013, 2019; Roberts et al., 2017a). In addition to it being located at a key geographical juncture, it also sits at a major biogeographic junction between the Sahara-Arabian and Afrotropical regions to the west and Palearctic and Sino-Japanese regions to the north (Watts, 1984; Holt et al., 2013; Blinkhorn et al., 2013). Archaeological research in South Asia over the past two decades has pointed to potential multiple, earlier routes of dispersal into the region (Petraglia et al., 2010; Boivin et al., 2013; Bae et al., 2017; Blinkhorn and Petraglia 2017), and emphasizing the varied and complex local patterns of technological and cultural change (Petraglia et al., 2010, 2012; Blinkhorn et al., 2013), as well as the diversity of the types of terrestrial environments, utilized by early humans (Blinkhorn et al., 2016; Roberts et al., 2015a, 2017b). This is in contrast to a prominent model that assumes a rapid, coastal *ca.* 60 ka dispersal of humans, associated with uniform technological features around the Indian Ocean Rim (Mellars, 2006; Mellars et al., 2013).

Research in Sri Lanka, an island at the southern tip of South Asia, has highlighted how early members of our species employed adaptive strategies to take full advantage of their environments such as tropical rainforests. Traditional anthropological and archaeological assumptions viewed rainforests as barriers to human occupation due to a scarcity of resources, including calorie-rich plants and large animals (Bailey et al., 1989; Gamble, 1993). Nevertheless, Sri Lanka has produced the earliest clear evidence for *Homo sapiens* fossils in tropical rainforest environments in South Asia (Kennedy, et al., 1987; Kennedy and Deraniyagala, 1989; Deraniyagala, 1992; Kennedy, 2000) as well as evidence for heavy reliance on rainforest resources, including specialized hunting of arboreal and semi-arboreal

fauna from ~45,000 years ago through to 3,000 years ago (Roberts et al., 2015a,b, 2017b; Wedage et al., 2019a) facilitated by microlith and osseous technologies (Deraniyagala, 1992, Wijeyapala, 1997, Perera et al., 2011, Wedage et al., 2019a; Langley et al., 2019). However, knowledge of the scale of Late Pleistocene tropical rainforest occupations in the region remains limited since multidisciplinary analyses of archaeological sequences are restricted to two sites: Fa Hien-lena, dated to *ca.* 45,000 years ago (Wedage et al., 2019a) and Batadomba-lena, dated to *ca.* 38,000-36,000 years ago (Roberts et al., 2015b).

Traditionally, a third site, Kitulgala Beli-lena, has been grouped with these other two sequences as a source of early human fossils (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989; Wijeyapala, 1997) and microlith adaptations (Deraniyagala, 1992). Yet, this site has been overlooked in recent debates given that existing radiocarbon dates place this sequence considerably later (31,000 years ago – Kourampas et al., 2009). Moreover, a lack of published zooarchaeology, archaeobotany (though see Kajale, 1989), and detailed technological analysis, as well as the fact that the site required re-dating using methods better equipped to deal with contamination in tropical environments (see Higham et al., 2008), have meant comparisons of Kitulgala Beli-lena to Fa Hien-lena and Batadomba-lena are somewhat superficial. Here, we present the results of renewed excavation and multidisciplinary analyses of materials recovered from Kitulgala Beli-lena. We present a revised stratigraphy for the site as well as new chronological information. Alongside detailed insights into prey choices, plant use, and sedimentary formation processes at the site, lithic data from the site indicates that Kitulgala Beli-lena was potentially part of a social network of technological procurement and production. In addition, our research highlights possible differential spatial use of cave and rockshelter sites in the Sri Lankan rainforest in the Late Pleistocene and Holocene. By placing our data from Kitulgala Beli-lena in its wider Sri Lankan and Asian context we are able to

present a more complete picture of Late Pleistocene and Holocene human adaptation and presence in this increasingly significant region for human evolutionary research.

2. Kitulgala Beli-lena Rockshelter

Kitulgala Beli-lena is located in the Kegalle district of Sri Lanka's Sabaragamuwa Province, approximately 85 km east of Colombo (Figure 1). With a *ca.* 30 x 15 m north facing entrance, the rockshelter is formed within a gneiss bedrock, part of the metamorphic terrain of Sri Lanka's Highland Complex (Cooray, 1984). Kitulgala Beli-lena is situated in the island's lowland Wet Zone with a mean annual precipitation between 2500-3500 mm/year (Dömros, 1974; Roberts et al., 2015b), surrounded by humid tropical rainforest. The rockshelter was first explored by P.E.P. Deraniyagala in 1960-1961, who excavated several test pits and noted an abundance of historic and prehistoric archaeological materials. However, no detailed description of this first investigation was ever published. Systematic excavation of the rockshelter continued in 1978 by the Department of Archaeology of the Government of Sri Lanka under the supervision of S.U. Deraniyagala. Excavations continued in 1979, 1983, 1985 and in 1986 (under W. H. Wijeyapala) (Figure 1). The Department of Archaeology, this time led by Oshan Wedage, carried out a small excavation of 1 m² in the southeast corner of the rockshelter in 2013. Collectively, these excavations sampled depths of more than 3 m of cultural deposits and produced a total of 25 radiocarbon dates (Table 1), indicating a chronology extending back to *ca.* 31,000 cal. years BP. Two thermoluminescence dates (17,217 ± 3300 and 18,565 ± 2610) have also been reported (Abeyratne, 1994).

Excavations of Terminal Pleistocene sediments of the site, with associated charcoal dated to 12,260 ± 870 years BP, had previously yielded several human remains including a partial skeleton of an adult of indeterminate sex, a skull of a child 10-11 years of age at the time of

death, bones and teeth from at least ten different individuals (Kennedy et al., 1987; Kennedy and Deraniyagala, 1989; Wijeyapala, 1997). Sparse microlithic tools, manufactured from quartz, were also recorded from the beginning of site occupation (Wijeyapala, 1997). However, these technologies, as well as osseous tools, were not systematically analysed. In 2017, a new excavation in Kitulgala Beli-lena was conducted by the Max Planck Institute for the Science of Human History and University of Sri Jayewardenepura in collaboration with the Department of Archaeology, Government of Sri Lanka. The aim of the excavation was to recover new materials to produce a refined chronology for the site, using appropriate pre-treatment methodologies for charcoal samples as well to conduct systematic zooarchaeological, archaeomalacological and archaeobotanical analyses. Three 1 x 1 m squares were opened in the inner western section of the rockshelter, close to the wall, following the grid laid out during the 1980s excavation (Figure 1). The excavation reached a final depth of 192 cm from the surface rockshelter deposits.

Table 1. Previous radiocarbon dates for Kitulgala Beli-lena (from Deraniyagala, 1992, Wijeyapala, 1997, Perera, 2010).

Stratum	Lab Code	^{14}C	cal. BP*
VIIa2	Beta 18448	3640 ± 60	4,150 - 3,829
VIIa1	PRL 1012	3170 ± 120	3,691 - 3,661
VIb1	Beta 18446	8160 ± 80	9,407 - 8,976
VIa1	Beta 18445	7040 ± 80	8,000 - 7,698
Va3	BS 287	$10,200 \pm 170$	12,517 - 12,493
Va3	BS 288	$10,280 \pm 170$	12,571 - 11,394
Va3	BS 289	$10,010 \pm 160$	12,156 - 11,146
Va3	PRL 861	$11,910 + 430/-410$	15,298 - 12,981
Va3	BS 290	$11,550 \pm 180$	13,751 - 13,076
Va3	Fra-91	$11,780 \pm 220$	14,155 - 13,151
Va3	BS-292	$11,570 \pm 210$	13,933 - 13,901
Va2	BS-292	$11,520 \pm 220$	13,825 - 12,901
Va1	BS-293	$12,240 \pm 160$	14,933 - 13,758
IVb3	Beta 33287	$11,860 \pm 70$	13,816 - 13,481
IVb2	BS-294	$11,750 \pm 390$	14,948 - 12,831
IVb2	Beta 33286	$13,150 \pm 80$	16,071 - 15,477
IIIc3	Beta 33285	$13,150 \pm 90$	16,084 - 15,435
IIIc2	Fra-163	$15,780 \pm 400$	20,086 - 18,236

IIIc2	Fra 164	16,400 ± 650	21,605 - 18,458
IIIc2	Beta 18443	18,050 ± 180	22,352 - 21,414
IIIc1	Beta 18442	17,810 ± 170	22,001 - 21,036
IIIb1	PRL 1013	17,870 +510/-530	22,862 - 20,411
IIIb1	Beta 18441	18,900 ± 350	23,666 - 22,024
IIIa3	Beta 33283	20,560 ± 130	25,190 - 24,370
IIIa2	Beta 18439	older than 26,425	-

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)

3. Methods

3.1 Excavation

The 2017 excavation of Kitulgala Beli-lena aimed to recover new archaeological material in order to refine/revise the chronology of the site and better understand human culture, technology, and subsistence strategies. The excavation was situated in the inner western section of the rockshelter, some 5 m from the wall. Following the excavations in the rockshelter in 1985, the exposed sections were covered by stone walls to preserve the integrity of the site. The only portion that was not protected was a 2 m² excavation square (grid code: G12-G11) which was sampled for micromorphology in 2005 and 2009 (Perera, 2010, Kourampas et al., 2009). The new excavation extended this unprotected square southward, opening excavation square G12 and the previously unexcavated squares H14 and I14 (Figure 1) and allowing for the correlation of the results to the micromorphological analyses of Kourampas et. al (2009).

Excavations were conducted using hand tools dividing artefacts and sediment samples into discrete sediment units, or subdividing discrete sediment units into 5cm arbitrary horizons, where single contexts were deeper than 5cm. Three dimensional recording of the excavated area, the interface between sediment deposits and major artefacts (>20 mm) was undertaken using a Leica Builder 505 total station. After removal, excavated sediments were placed on

polythene sheeting and a sub-sample was taken for flotation. A total of 1120 liters of sediment were floated (using a 250 micron mesh) during the excavation. The rest of the excavated sediments were wet sieved to allow for the recovery of cultural materials. In addition, samples of approximately 100 g were recovered at 5 cm intervals to enable a range of sediment analyses (including ongoing analyses i.e. laser particle size analyses, phosphate analyses etc.).

3.2 Radiocarbon dating

Fourteen charcoal fragments recovered during excavation were submitted for dating to the Oxford Radiocarbon Accelerator Unit. The charcoal samples were prepared using the acid–base oxidation/stepped combustion (ABOx-SC) protocol (Bird et al., 1999; Higham et al., 2008). Of these, 13 samples yielded ^{14}C measurements that were calibrated using the IntCal13 calibration curve and the OxCal 4.3 programme (Reimer et al., 2013; Bronk Ramsey 2017).

3.3 Zooarchaeological analysis and osseous technology analysis

All recovered bone fragments from the 2017 excavation of Kitulgala Beli-lena were analysed, including fragmentary remains as well as diaphyses and rib shafts. All specimens were sorted, counted, and measured (length, width, and thickness) using a digital caliper (Mitutoyo 500–463). Identified specimens were recorded in detail using codes for anatomic zones following a zonation system modified from Dobney and Reilly (1988) to allow for the description of fragmentation patterns. Diagnostic skeletal elements were identified using comparative vertebrate specimens from the Field Museum of Natural History and American Museum of Natural History and from the Laboratory of Comparative Anatomy of the Muséum national d'Histoire naturelle (MNHN). Naming of identified taxa follows the nomenclature published by Wilson and Reeder (2005). The identified taxa were classified to size class based on live weight following a modification of the criteria established by Thomas (1969) and Grayson

(1984): (a) micromammals: 100 g to 1 kg, (b) small mammals: 1 kg to 25 kg, (c) large mammals class 1: 25 kg to 200 kg, (d) large mammals class 2: 200 kg to 1000 kg, and (e) large mammals class 3: > 1000 kg.

All fragments were examined for natural, animal, and anthropic modifications, including weathering (Behrensmeyer, 1978; Andrews, 1995), abrasion (Shipman and Rose, 1988), burning, staining, and butchery marks (Fernandez-Jalvo and Andrews, 2016). Bone surface modifications, including traces of bone tool manufacture, were recorded/observed using an Olympus BX53 light microscope. Bone artefacts were further examined under a Keyence VHX-6000 digital microscope to record traces of use. Bone surface modifications resulting from tool production and use were identified following published criteria (i.e. Shipman and Rose, 1988; Blasco et al., 2008; Bradfield and Brand, 2015; Langley et al., 2016).

In terms of zooarchaeological quantifications, the minimum number of element (MNE) and minimum number of individual (MNI) counts were calculated following a modification of Dobney and Rielly's (1998) zonation system. This system is based on the recording of distinct morphological zones in a skeletal element. The MNE was taken as the total number of non-overlapping zones (i.e., greater than 50% of the diagnostic zone present) for every skeletal element of a taxon. The highest MNE value, considering side and age (epiphyseal fusion and dental wear, following Klein and Cruz-Urbe (1984), was used to estimate the MNI. The MNE counts were converted to minimum animal unit (MAU) values by taking into account the number of times the element occurs in the skeleton. The normalized MAU values (% MAU) were used to compare skeletal part representation in the different phases of cave occupation (Lyman, 1994).

3.4 Invertebrate analysis

The invertebrate assemblage of Kitulgala Beli-lena consists of all remains collected during the 2017 excavation of the site, including fragmentary specimens recovered from dry and wet sieving of sediments. Prior to analysis, all samples were washed to remove excess sediment and air-dried for 24-48 hours. As a physical comparative reference collection was not available for specimen identification, all taxonomic attributions were made following the descriptions and/or illustrations provided in Hausdorf and Perera (2000), Naggs and Raheem (2000), Raheem and Naggs (2006) and Starmuhlner (1974). Recent correspondence with Dr Dinarzarde Raheem (Natural History Museum, London) indicates that significant taxonomic revision of the Sri Lankan terrestrial and freshwater mollusc fauna is needed.

Although the resources currently available are useful for identifying genera and are likely to be of limited value for species level-identification, specimens were attributed to taxonomic categories (e.g. to species, genus, or family) based on the preservation of identifiable diagnostic features. Taphonomic indicators, such as dissolution, burning, and predatory boring, were also noted. Although the assemblage was recorded in such a way so as to enable the calculation of the MNI, due to the small sample size the quantification measures reported here are restricted to NISP and weight (in grams).

3.5 Archaeobotanical analysis

The archaeobotanical assemblage analysed in this study comprises of materials from flotation samples from five sedimentary contexts spanning the Pleistocene sequence of Kitulgala Beli-lena, namely contexts 10, 17, 21, 24, 23. The flotation samples were sieved into >4mm, 2-4mm, 1-2mm, and <1mm fractions. The >4mm and 2-4mm fractions were sorted under low magnification (x8–x40) using an Olympus SZ61 stereozoom microscope and the 1-2mm fraction was scanned for any smaller remains. Analysis of this material is ongoing and subject

to the establishment of a comparative ethnobotanical reference collection for Sri Lanka. Taxonomic identifications where possible were based on published descriptions (e.g., Kahn and Ragone 2013; Kajale 1988; Levin 2015) and available comparative botanical material in the University of Queensland's Archaeobotany Laboratory.

3.6 Lithic analysis

The technological analysis of the lithic assemblages was performed using the *chaîne opératoire* concept, a methodological framework that defines the reconstruction of the various processes of flake production from the procurement of raw materials through to discard (Lemonnier, 1986; Pelegrin et al., 1988). The assemblages were firstly discriminated by raw material units, defined according to variety of stone and macroscopic features including type of cortex, colour, grain size, and texture (Roebroeks, 1988). The technological features were then reconstructed through the diacritic analysis of the scar pattern organization on the cores' flaking surfaces and on the flakes' dorsal side. Previous studies on the lithic collections in Sri Lanka report the extensive use of the bipolar method (Lewis, 2017; Wedage et al., 2019a; 2019b). In order to address the variability of this lithic reduction strategy, the analysis was performed following more recent definitions based on experimental knapping data (Crabtree, 1972; de la Peña, 2015; Donnart et al., 2009; Mourre, 1996). The flake assemblages were classified by dimensional criteria and only the lithic items greater than 1 cm were analysed. Bladelets are considered elongated blanks in which the ratio length to width is ≥ 2 , and with a percussion axis length of less than 4 cm (Petraglia et al., 2009). A distinction has not been made between bladelets produced from true bladelet cores and flake-bladelets. Siret knapping accidents were distinguished following the criteria of Mourre (1996) whereas *bâtonnet* flakes (or bipolar spalls) and splinter flakes were defined following Brun-Ricalens (2006).

4. Results

4.1 A Revised Chronostratigraphy for Kitulgala Beli-lena

The fill of Kitulgala Beli-lena consists of *ca.* 192 cm of stratified detrital sediments deposited on a heavily weathered and phantomed gneiss bedrock over the last *ca.* 44,000 years. Thirteen new radiocarbon dates (Table 2) anchor the stratigraphy and resolve it into four phases, each corresponding to a major period of human occupation of the rockshelter (Figure 1). The sedimentary layers excavated in 2017 correspond to those recorded during the previous excavation of squares H6 and I6 as well as the micromorphological sequence reported by Kourampas et al. (2009) (Table 3).

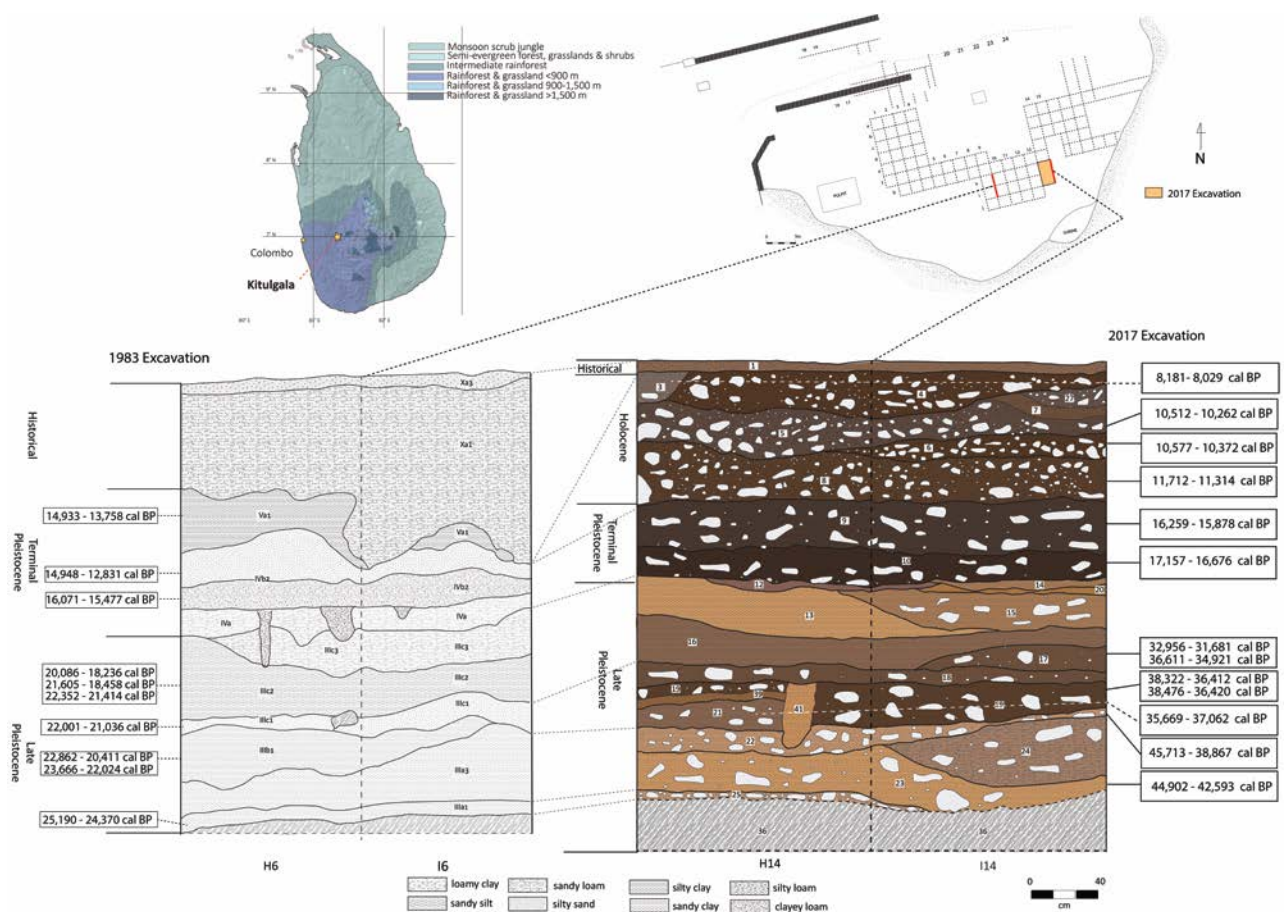


Figure 1. Map of Sri Lanka showing the location of Kitulgala Beli-lena and the country's vegetation zones (Ashton et al., 1987, Erdelen, 1988). Location of the 2017 excavation squares and comparison of the 1983 (Wijeyapala, 1997) and 2017 stratigraphy.

Table 2. New radiocarbon dates from the 2017 excavation of Kitulgala Beli-lena

Context	Labcode (OxA)	Measured Date	Calibrated (cal. BP)*
3	37930	7,309 \pm 34	8,181- 8,029
5	37932	9,230 \pm 40	10,512 - 10,262
6	37933	9,280 \pm 37	10,577 - 10,372
8	37934	10,015 \pm 39	11,712 - 11,314
9	37935	13,360 \pm 50	16,259 - 15,878
10	37936	13,960 \pm 50	17,157 - 16,676
17	37808	28,420 \pm 180	32,956 - 31,681
17	37789	31,880 \pm 390	36,611 - 34,921
19	37809	33,120 \pm 330	38,322 - 36,412
19	37810	33,230 \pm 390	38,476 - 36,420
21	37724	32,410 \pm 260	35,669 - 37,062
22	X-2782-17	37,500 \pm 1700	45,713 - 38,867
23	37483	39,900 \pm 700	44,902 - 42,593

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013).

Table 3. Major phases of Kitulgala Beli-lena occupation.

Occupational Phase	Sedimentary Context (2017)	Dates (cal. BP)	Sedimentary Stratum (1983)	Dates (cal. BP)*
Historical	1	-	Xa3	-
Holocene	3	8,181- 8,029	-	-
	5	10,512-10,262		
	6	10,577- 0,372		
	8	11,712-11,314		
Terminal Pleistocene	9	16,259 -15,878	IVb3	13,816-13,481;
			IVb2	14,948-12,831
	10	17,157 -16,676	IVb2	16,071-15,477
Late Pleistocene			IVa	
	12, 13, 14, 15, 20	-	IIIc3	16,084-15,435;
			IIIc2	20,086-18,236;
				21,605-18,458;
				22,352-21,414
	17	32,956 - 31,681;	IIIc1	22,001-21,036
		36,611 - 34,921		
	19	38,322 - 36,412;		
		38,476 - 36,420		
	21	35,669 - 37,062		
	18, 39, 41	-		
	22	45,713 - 38,867	IIIa3	25,190 - 24,370
	23	44,902 - 42,593		
	24	-		
	25	-	IIIa2	older than 26,425†

*All samples were calibrated using the OxCal 4.3 software (Bronk Ramsey 2017) and IntCal calibration curve (Reimer et al., 2013)

†uncalibrated

303 *Late Pleistocene Phase*

304 The Late Pleistocene phase of the rockshelter represents intermittent/episodic human
305 occupation, from around *ca.* 44,000 to 31,000 cal. BP. It is characterized by pebbly clayey
306 loams with angular gneiss slabs and subhorizontal layers of yellowish brown, sandy clay to
307 sandy silt deposits. Just above the gneiss bedrock is a *ca.* 10 cm clast supported conglomerate
308 with well-rounded imbricated pebbles that is hypothesized (Wijeyapala, 1997; Kourampas,
309 2009) to have been deposited by a stream that at the present flows 60 m below the level of the
310 rockshelter's entrance. This layer, notably devoid of any cultural materials, is overlain by a
311 series of sandy loam and sandy clay deposits containing angular gneiss slabs and abundant
312 charcoal.

313 Kourampas et al. (2009) suggest that these layers most likely represent an admixture of roof
314 fall and colluvial deposits reworked by bioturbation and rockshelter floor processes including
315 trampling and surface runoff. The first in the series, Context 23, returned dates as early as
316 42,593-44,902 cal. BP. These sedimentary layers, referred to as phases IIIa(2)-IIIc(3) by
317 Wijeyapala (1997), were previously dated to 25,190 - 18,236 cal. BP. New dates now place
318 these layers as being deposited between *ca.* 44,902-31,600 cal. BP (Figure 1). Evidence of
319 human activities in the Late Pleistocene phase includes artefacts (ochre fragments and stone
320 tools) and macrobotanical remains. No faunal remains were recovered in the Late Pleistocene
321 layers during the 2017 excavations.

322 *Terminal Pleistocene Phase*

323 The Terminal Pleistocene phase of site occupation is characterized by dark greyish brown
324 sandy loam and silty clay deposits notable for a heavy concentration of quartz microliths and
325 macrobotanical remains (e.g. context 9-10). This *ca.* 30 cm phase of occupation correlates to
326 sedimentary layers IV and V from the 1983 excavation which were dated to 13,600-12,100
327 cal. BP (Wijeyapala, 1997) and contains the densest occupation debris in terms of charcoal

and lithic materials. Discrete patches of burnt sediments and ashes point to possible hearths within the layers. Angular gneiss slabs most likely from roof fall or wall disintegration are also abundant in these layers. Charcoal from these layers recovered from the 2017 excavation returned dates between 17,157-11,314 cal. BP. Kourampas (2009), in his micromorphological analyses of the stratigraphy from the 1986 excavation, interpreted these layers as resulting from accelerated sedimentation brought about by human activity, high rates of colluvation, and accelerated water seepage.

Previous reports (Deraniyagala, 1992; Wijeyapala 1997) noted that faunal remains (both vertebrate and invertebrate) were recovered from the Terminal Pleistocene layers of Kitulgala. However, not a single piece of faunal material was recovered from the 2017 excavation. Kourampas et al. (2009) also reported an absence of microscopic bone fragments in the micromorphological sections from these layers. It is unlikely that the absence of animal bones and molluscan remains from the Late Pleistocene and Terminal Pleistocene phases of the site resulted from taphonomic processes as abundant macrobotanical remains and unweathered quartz flakes were recovered in the same layers.

Holocene Phase

The Holocene Phase of Kitulgala consists of at least six distinct sedimentary layers with abundant charcoal, quartz microlith, and ochre content. These layers, previously dated to 9,070-3,550 cal. BP (layer VI to VII), have been re-dated to 10,577-8,029 cal. BP. Unlike the underlying sedimentary layers, the Holocene layers yielded numerous faunal materials. *In situ* hearths with burnt seeds and animal bone fragments were also recorded. The lowermost layer, a compact mid-yellowish brown sandy loam, contains frequent mid-sized (up to 15 cm) angular gneiss slabs suggestive of a roof-fall episode that happened sometime during the onset of the Holocene. Overlying this is a series of almost horizontal loamy clay and silty sand layers rich in debris from human activity.

Historical Phase

A *ca.* 10 cm silty sand deposit represents the Historical Phase of occupation of Kitulgala Beli-lena. Much thicker near the entrance (i.e. *ca.* 50 cm in the previous excavation of H10/I10), this layer has been interpreted as reworked sediment and residue resulting from the extraction of guano-rich deposits used as fertilizer in nearby rubber plantations during colonial times (Wijeyapala, 1997). It is chronologically mixed, containing potsherds and abundant mollusc fragments as well as animal bones and quartz flakes most likely reworked from earlier phases of site occupation. The guano extraction digging had cut through Early Holocene deposits in some parts of the site (Wijeyapala, 1997). Kourampas et al. (2009) noted that the historical deposit did not penetrate below Mid-Holocene levels in the profile they studied. The new dates, however, suggested that much of the mid-Holocene deposits of Kitulgala Beli-lena were removed during the historical phase.

4.2 Vertebrate Fauna

A total of 5502 animal bone fragments were recovered from the 2017 excavation of Kitulgala Beli-lena. As noted above, all of the vertebrate remains were recorded from sedimentary contexts dated to the Early Holocene. Small mammals (< 25kg) dominate the faunal assemblage, accounting for 70.5% (Total number of fragments, TNF= 3859, Number of identified specimens, NISP=2156) of the remains recorded, suggesting deliberate targeting of these animals by the people that settled in Kitulgala (Table 4, Figure 2). Large mammals account for 3.9% of the recovered animal bones and micromammals (mostly murids and bats) account for 10.7%. Reptiles (11.1% NISP), fish (4.8% NISP) and birds (2.1% NISP) were also identified in the assemblage.

Table 4. Vertebrate remains recovered from the 2017 excavation of Kitulgala Beli-lena.

Context	Unidentifiable Bone Fragments					NISP	% NISP	TNF
	Micromammal	Small Mammal	Large Mammal	Non-Mammals	Total			
2	54	124	24	22	224	345	60.6%	569
3	61	244	45	49	399	621	60.9%	1020
4	68	327	38	63	496	714	59.0%	1210
5	41	341	27	5	414	421	50.4%	835
6	10	92	10	22	134	198	59.6%	332
7	45	287	14	20	366	321	46.7%	687
27	32	288	12	46	378	471	55.5%	849
Total	311	1703	170	227	2411	3091	56.2%	5502

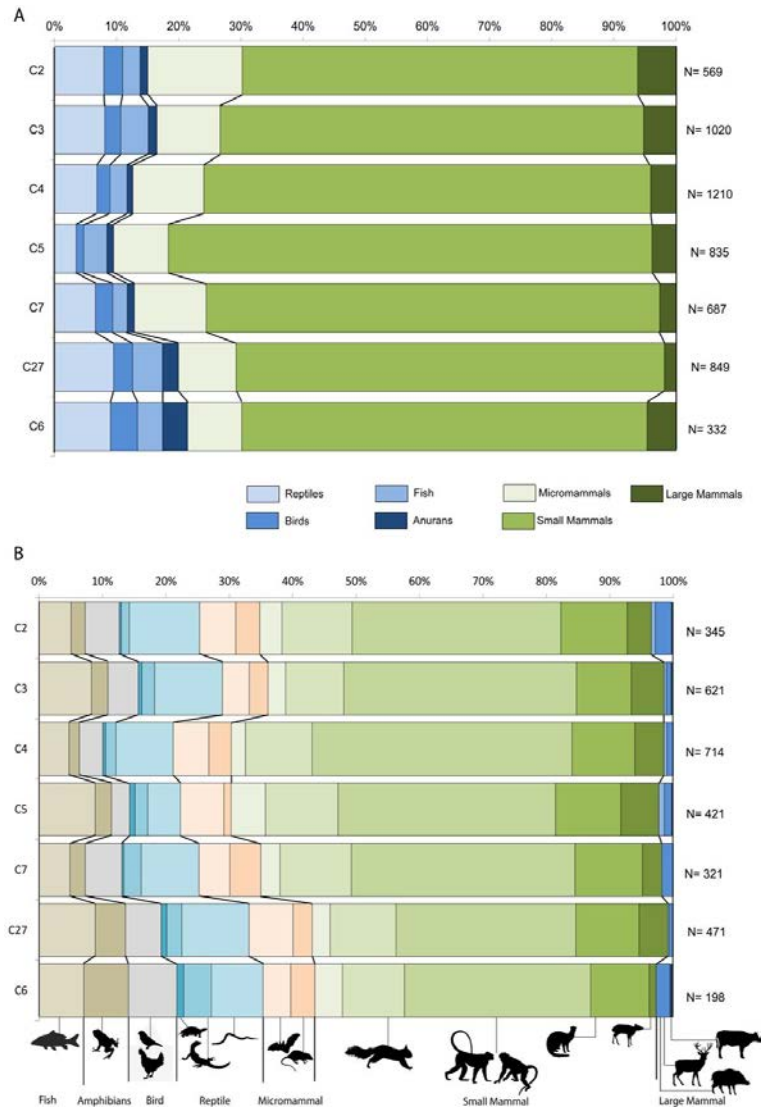


Figure 2. Distribution of animal taxa identified in different Holocene sedimentary contexts of Kitulgala Beli-lena based on the total number of bone fragments recovered (TNF, A) and number of identified specimens (NISP, B).

419 **Table 5.** Number of identified specimens and minimum number of individuals of the different vertebrate taxa identified in Kitulgala Beli-lena.

420

Class	Order	Family	Taxon	TOTAL														
				2		3		4		5		6		7		27		NISP
Actinopterygii	Cypriniformes	Cyprinidae	8	-	28	-	21	-	27	-	7	-	10	-	26	-	127 (4.1%)	-
	Siluriformes	Siluridae	2	1	3	1	4	1	2	1	1	1	1	1	5	1	18 (0.6%)	7
			1	1	1	1	-	-	1	1	-	-	-	-	1	1	4 (0.1%)	4
Amphibia	Anura	2	1	7	2	11	4	9	3	8	3	4	1	10	3	51 (1.6%)	17	
Aves	5	-	5	-	4	-	4	-	4	-	2	-	5	-	5	-	30 (1.0%)	-
	Apodiformes	1	1	3	1	-	-	1	1	3	1	2	1	1	1	1	11 (0.4%)	6
	Galiformes	3	1	4	2	2	1	1	1	2	1	4	2	4	1	20 (0.6%)	9	
	Strigiformes	1	1	-	-	-	-	1	1	-	-	-	-	1	1	3 (0.1%)	3	
Reptilia	Testudines	1	1	3	1	3	1	3	1	2	1	1	1	4	1	17 (0.5%)	7	
	Squamata	2	1	8	2	4	1	3	2	2	1	5	2	6	2	30 (1.0%)	11	
	Agamidae	1	1	2	1	5	2	4	1	4	1	3	1	4	1	23 (0.7%)	8	
	Geckonidae/Scleridae	1	1	1	1	2	1	-	-	2	1	1	1	1	1	8 (0.3%)	6	
	Pythoridae	21	1	37	2	32	1	10	1	8	1	16	1	28	1	152 (4.9%)	8	
	Colubridae/Viperidae	14	1	21	2	29	2	8	1	7	1	14	1	21	2	114 (3.7%)	9	
Mammalia	Primates	92	7	173	12	254	18	105	11	46	5	104	9	118	10	892 (28.9%)	72	
	7	1	18	3	14	2	10	1	6	1	1	9	1	10	2	74 (2.4%)	11	
	5	1	8	2	9	1	5	1	2	1	3	1	3	1	3	35 (1.1%)	8	
	Rodentia	10	2	13	2	12	2	18	3	8	1	10	2	11	3	82 (2.7%)	15	
	Hystriidae	76	8	157	15	127	10	109	12	39	4	41	5	88	6	637 (20.6%)	60	
	Sciuridae	2	1	3	2	4	2	4	2	1	1	1	1	1	1	17 (0.5%)	10	
	Muridae	12	2	16	3	24	5	4	2	7	2	16	3	14	4	93 (3.0%)	21	
	Leporidae	1	1	-	-	-	-	1	1	-	-	-	-	2	1	4 (0.1%)	3	
	Chiroptera	18	3	22	4	42	5	24	3	8	2	15	3	32	5	161 (5.2%)	25	
	Hippocridae	1	1	-	-	-	-	-	-	-	-	1	1	-	-	2 (0.1%)	2	
	Rhinolophidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2 (0.1%)	2	
	Carnivora	34	4	45	4	64	5	35	4	22	2	37	2	49	4	286 (9.3%)	25	
	Mustelidae	1	1	4	1	3	1	3	1	-	-	1	1	1	1	13 (0.4%)	6	
	Artiodactyla	12	4	30	4	33	4	21	2	6	2	10	2	21	3	133 (4.3%)	21	
	Tragulidae	2	1	2	1	3	1	3	1	-	-	-	-	-	-	11 (0.4%)	5	
	Suidae	8	2	4	1	7	2	4	1	4	1	6	1	3	1	36 (1.2%)	9	
	Cervidae	1	1	2	1	-	-	1	1	1	1	-	-	-	-	5 (0.2%)	4	
	Bovidae	1	1	2	1	-	-	1	1	1	1	-	-	-	-	5 (0.2%)	4	
	Total	345	52	621	71	714	73	421	60	198	35	321	44	471	59	3091	394	

0-20

21-40

41-60

61-80

81-100

>100

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4-6

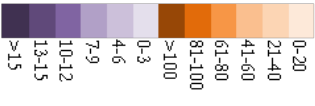
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421



422 From the 5502 vertebrate remains recovered from the site, 3091 (56.2%) can be confidently
423 assigned to family, genus, or species (Table 5). Cercopithecoid monkeys dominate the Early
424 Holocene assemblage of the site, with a total of 1001 remains from at least 91 individuals
425 recorded. Both cercopithecines (macaque) and colobines (langurs) were identified in the
426 assemblage based on teeth and certain post-cranial elements. However, the high degree of
427 fragmentation prohibits confident identification of these elements to species. Only 74 (7.4 %,
428 MNI= 11) specimens can be confidently identified as representing *Macaca sinica* and 35
429 (3.5%, MNI=8) were identified as from langurs (*Semnopithecus/Trachypithecus*). All skeletal
430 elements were represented in the assemblage suggesting that complete monkey carcasses
431 were brought in and processed on the site.

432 Distal articular ends of long bones and metapodials and other dense skeletal elements (carpals
433 and tarsals) as well as teeth are slightly over-represented in the assemblage. In terms of
434 anthropogenic signature, 35.8% of the identified cercopithecoid specimens exhibited evidence
435 of burning. Cutmark frequency is relatively low, with only two specimens (a distal humerus
436 and proximal femur fragment) exhibiting evidence of butchery. Age-at-death profile of
437 cercopithecoid monkeys in the assemblage based on dental wear suggests deliberate targeting
438 of sub-adults and adults. Most of the aged individuals fall within the age category J7 to A3
439 outlined by Ingicco et al., (2012) for the genus *Trachypithecus*. These individuals are of full
440 sexual maturity, with completely erupted third molar (aged between 3 and 5 years old,
441 Harvati, 2000; Bolter, 2011).

442 Sciurids represent the second most common taxa in the Holocene faunal assemblage of
443 Kitulgala with a total of 654 dental and skeletal elements identified. 97.4% of the elements
444 correspond in terms of size and morphology, particularly for dental elements, to comparative
445 specimens of the grizzled giant squirrel (*Ratufa macroura*) while the rest (NISP= 17)
446 represent flying squirrels (*Petinomys/Petaurista*). Burning and calcination were observed in

447 12.3% and 5.4% of the identified sciurid specimens, respectively. Other small mammals
448 identified in the assemblage include civet cats (9.3% NISP, MNI=25), otters (0.4% NISP,
449 MNI=6), chevrotains (4.3% NISP, MNI=21) and porcupines (2.7% NISP, MNI=15). Similar
450 to cercopithecids, these animals are represented mostly by dental and dense postcranial
451 elements.

452 A total of 222 specimens representing large mammals were recorded in the assemblage. From
453 these, 23.4% can be assigned confidently to taxa. These include 11 (0.4% NISP, MNI=5) suid
454 specimens, 36 (1.2% NISP, MNI=9) cervid and 5 (0.2% NISP, MNI=4) bovid fragments.
455 Anthropogenic modifications were mostly restricted to burning (12.6%). Butchery marks were not
456 observed in any large mammal bone fragments, albeit a proximal cervid metatarsal exhibited
457 evidence of impact fractures and two bovid and one cervid metapodial fragments showed
458 evidence of modifications consistent with tool/artefact production.

459 Non-mammalian fauna represents 15.2% (19.7% NISP) of the animal remains from the site.
460 Fish (NISP=149) are represented mostly by cyprinids (carps), identified from pharyngeal
461 teeth and certain cranial elements. Silurid (catfish) specimens (spine) were also identified,
462 albeit in very low frequency (NISP=4). Reptiles (11.1% NISP) on the other hand are
463 represented by varanids, pond/river turtles, agamid/iguanid lizards, pythons and colubrid
464 snakes (Table 5). The fish bones recorded in the site exhibited a high degree of burning
465 (40.9%). Likewise, several reptile bone fragments, particularly varanids and *Python*,
466 exhibited evidence of burning and calcination (11%), suggesting that they were probably also
467 utilized as a food source. Although bird skeletal elements are present in all sedimentary
468 contexts dated to the Holocene (2.1% NISP), only 20 (23.8%) fragments can be confidently
469 identified to taxa. These include owls (Strigidae), swifts (Apodidae) and jungle fowls
470 (Phasianidae).

Several animal taxa in the assemblage, such as frogs (1.6% NISP) and micromammals (<1kg) including murids (3% NISP) were most likely accumulated by non-human cave dwelling species (i.e. raptors). This is in addition to the colubrid snakes and small agamid lizards mentioned earlier. Swifts and bats (5.6%), on the other hand, most likely represent the rockshelter's natural faunal communities.

4.3 Osseous Technology

A total of 21 (0.38% of the bone assemblage studied) finished tools manufactured from small mammal long bones were identified in the site, including 10 finished unipoints, seven bipoints, and four geometrics (Figure 3). Morphological features retained in some of the unipoints in the assemblage suggest that they were manufactured from cercopithecoid fibulae (Figure 3A) and ulnae (Figure 3B). The bipoints and the geometrics (Figure 3C-G), on the other hand, were most likely manufactured from cercopithecoid humerus or femur shaft fragments. However, further studies are needed to confirm this. At Fa Hien-lena, the bipoints and geometric bone tools from the Terminal Pleistocene and Early to Mid-Holocene layers were manufactured from cercopithecoid femur shaft fragments, based on the presence of blanks and unfinished tools (Wedage et al., 2019; Langley et al., 2019).

In terms of typology, the osseous tools recorded in Kitulgala Beli-lena are identical to those identified at Fa Hien-lena (Wedage et al., 2019a; Langley et al., 2019) and Batadomba-lena (Perera et al., 2011). The unipoints exhibit side notches suggesting that they were hafted to a shaft by ligature. These hafted bone points, again like those found in Fa Hien, most likely represent projectile points that were used by hunter-gatherers to selectively target certain arboreal animals (Wedage et al., 2019a; Langley et al., 2019). This is also consistent with the high-impact fracture observed in some of these specimens. However, unlike in Fa Hien-lena where 1.7% (N=246) of the faunal remains studied exhibited modifications consistent with

tool manufacture (grinding/polishing) (Wedage et al., 2019a), only finished tools were identified in Kitulgala Beli-lena. This suggests that the tools were not manufactured in the site, or at least in this part of the rockshelter.



Figure 3. Osseous tools manufactured from cercopithecoid appendicular skeletal elements recovered during the 2017 excavation of Kitulgala Beli-lena (A-B unipoints C-G bipoints). . Scale bars in microphotographs= 1 cm.

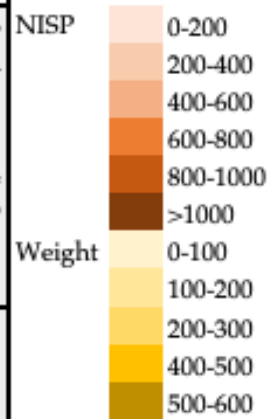
In addition to finished tools manufactured from small mammal bones, three bone tool fragments manufactured from cervid metapodial shafts were also recorded in the Holocene layers of the site. The fragments represent scraper and spatula-type tools, again similar to those recorded in Fa Hien-lena. The use wear on the edges of the tools identified in Kitulgala resemble the use wear of flaked tools recorded in Fa Hien-lena, such as striations suggestive of use as scrapers (Langley et al., 2019). Overall, the similarity of the osseous tools recovered from Kitulgala Beli-lena to those from Fa Hien-lena as well as those from Batadomba-lena suggests a shared technology that facilitated hunting and foraging in the rainforest environments of Sri Lanka.

4.4 Invertebrate Fauna

The total data for the invertebrate assemblage recovered from the 2017 excavation of Kitulgala Beli-lena is presented in Table 6, listing the taxonomic categories and total quantification data (NISP and weight) for each. The sample size reported here is relatively small, with a total NISP of 3799 and total weight of 2002.90g (or *ca.* 2kg). Similar to animal bones, the invertebrate remains were recovered only in layers dating to the Holocene and no specimens were recovered from Pleistocene contexts.

Table 6. Taxonomic categories and total quantification data of the invertebrate remains from Kitulgala Beli-lena.

Habitat	Family	Taxon	NISP	%NISP	Wt (g)	%Wt
Freshwater	Paludomidae	<i>Paludomus</i> spp.	1527	40,19	521,89	26,06
		<i>Paludomus bicinctus</i>	648	17,06	465,16	23,22
		<i>Paludomus chilinoideis</i>	118	3,11	99,79	4,98
		<i>Paludomus loricatus</i>	62	1,63	29,86	1,49
		<i>Paludomus neritoides</i>	230	6,05	219,17	10,94
		<i>Paludomus solidus</i>	241	6,34	240,22	11,99
		<i>Paludomus sulcatus</i>	244	6,42	149,65	7,47
	Unionidae	<i>Lamellidens</i> sp.	6	0,16	3,3	0,16
Terrestrial	Acavidae	Acavidae	366	9,63	183,59	9,17
		<i>Acavus</i> spp.	18	0,47	13,42	0,67
		<i>Acavus haemostoma</i>	1	0,03	12,2	0,61
		<i>Acavus superbus</i>	8	0,21	45,32	2,26
		cf. <i>Oligospira</i> sp.	3	0,08	0,97	0,05
	Cyclophoridae	<i>Cyclophorus</i> spp.	2	0,05	1,86	0,09
		<i>Cyclophorus menkeanus</i>	2	0,05	4,98	0,25
Indeterminate		Indet Crab	1	0,03	0,88	0,04
		Indet Landsnail	2	0,05	0,13	0,01
		Indet Shell	320	8,42	10,51	0,52
Total			3799		2003	



Breaking down the identified taxonomic groups, there is one category at the family level (9.63% NISP, 9.17% Wt), five categories at the genus level (40.96% NISP, 27.03% Wt), nine categories at the species level (40.91% NISP, 63.23% Wt), and three indeterminate categories (8.50% NISP, 0.58% Wt). The latter category encompasses indeterminate crab, land snail, and

shell, all of which do not retain key characteristics for identification beyond these broad attributions. Figure 4 graphs the taxonomic categories in descending order (highest to lowest) by %NISP (Figure 4A) and %weight (Figure 4B). Taxonomic rank order varies based on the quantification measure used, a factor that relates to shell size and morphology, robusticity, and also likely the differential degree of taphonomic modification within and between taxa. Regardless of the quantification measure used, the dominant taxa are the Paludomidae (freshwater gastropods) and the Acavidae (terrestrial gastropods). In many respects this is not unexpected, particularly given the similar trends reported for the Batadomba-lena rockshelter invertebrate assemblage (Perera et al. 2011). This dominance is also apparent when the assemblage is rank ordered by family (Figures 5A and 5B), where the Paludomidae and Acavidae are ranked first and second, followed by the indeterminate categories, by both %NISP and %weight. In combination with the occurrence of freshwater Unionidae bivalves, these data indicate the presence of flowing freshwater and lowland rainforest habitats around Kitulgala Beli-lena during the Holocene.

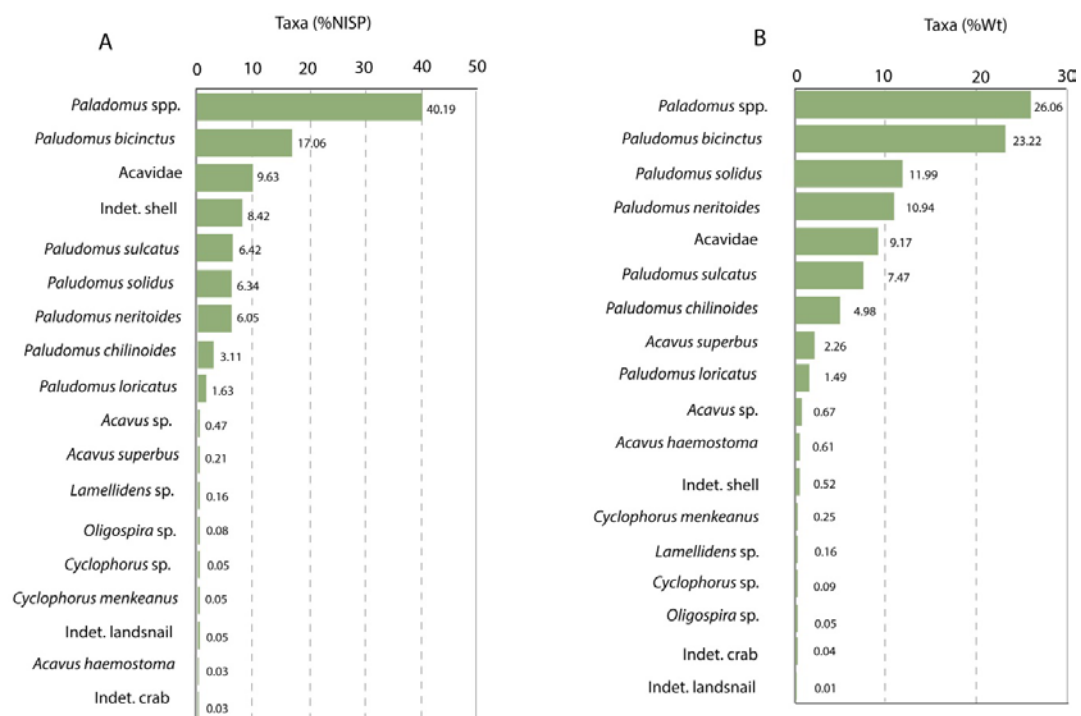


Figure 4. Kitulgala Beli-lena mollusc taxa by %NISP (A) and %Weight (B).

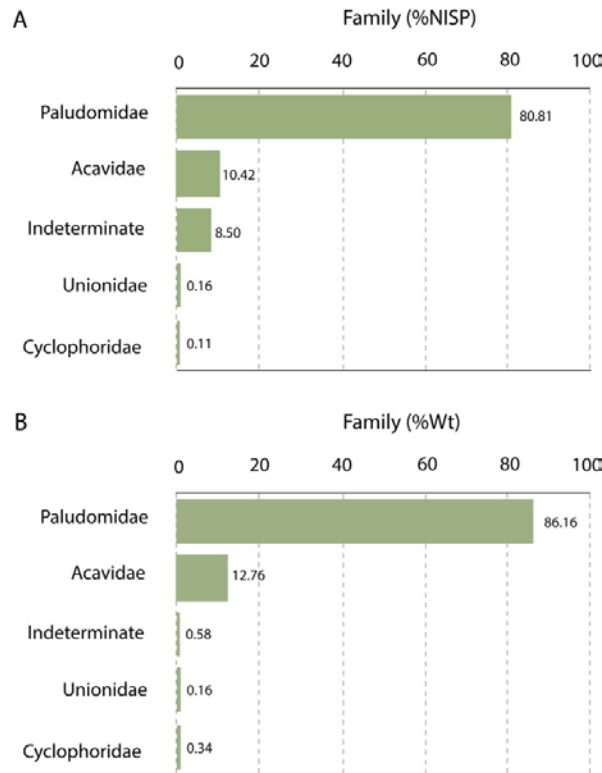


Figure 5. *Kitulgala Beli-lena* mollusc taxa at the family taxonomic level by %NISP (A) and %Weight (B).

The distribution of the freshwater and terrestrial molluscs by context is presented in Table 7.

These data are based on family or genus level, to account for some of the issues surrounding accurate identification to species level noted earlier. Based on these data, there would appear to be a level of consistency in taxonomic representation and habitat exploitation throughout the Holocene sequence at Kitulgala Beli-lena. The *Paludomus* spp. (range 76.9-86.3% NISP) and Acavidae (range 8.4-13.7% NISP) dominate the assemblage and occur relatively consistently across these contexts, with the freshwater bivalve *Lamellidens* sp. and the terrestrial gastropod *Cyclophorus* spp. occurring at very low percentages. The ratio of freshwater to terrestrial molluscs through the sequence also stays relatively consistent as a result, ranging between 6.2 and 7.4 in contexts 7/5, 4, 3 and 2, with a minor increase in freshwater taxa occurring in context 27 (with a ratio value of 9.7).

607 **Table 7.** *Kinulgala Beli-lena taxonomic distribution at family or genus level by sedimentary context (contexts 7 and 5 combined).*
608

Habitat	Taxon	Context 2		3		4		27		7/5	
		NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Freshwater	<i>Paludomus</i> spp.	349	84.91	1328	80.68	473	76.91	756	80.68	164	86.32
	<i>Lamellidens</i> sp.							6	0.64		
Terrestrial	Acavidae	49	11.92	178	10.81	64	10.41	79	8.43	26	13.68
	<i>Cyclophorus</i> spp.	1	0.24	2	0.12	1	0.16				
Total Context NISP		411		1646		615		937		190	
Freshwater:Terrestrial Ratio		6.98		7.38		7.28		9.65		6.31	

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These data suggest that there was a consistent focus on clean, flowing freshwater environments for the exploitation of molluscan resources, with some exploitation, albeit to a lesser extent, on lowland rainforest habitat gastropods. At Batadomba-lena, analyses of the invertebrate sample indicate that there was an increase in mollusc deposition after *ca.* 16,000 cal. BP, with freshwater taxa increasing and terrestrial taxa decreasing into the terminal Pleistocene (Perera et al. 2011). While the Kitulgala Beli-lena molluscan assemblage does not extend beyond the Holocene, the dominance of the freshwater taxa would appear to correspond with the expectations derived from the molluscan faunal shifts seen at Batadomba-lena rockshelter. The Kitulgala Beli-lena invertebrate faunal assemblage presents a similar range and distribution of freshwater and arboreal/terrestrial taxa to that seen in other cave sites in southwest Sri Lankan rainforest environments, particularly Batadomba-lena rockshelter.

4.5 Plant Remains

Preliminary assessment of the macrobotanical assemblage from the Pleistocene sedimentary contexts of Kitulgala Beli-lena revealed the presence of charred plant remains in all contexts analysed. These remains included charred fragments of wood, nutshell, fruits, and seeds. Overall, preservation in these contexts is limited with the macroremains generally exhibiting a high degree of fragmentation. The identification of these remains is ongoing however initial assessment indicates the likely presence of economic taxa including cf. *Artocarpus* sp. (breadfruit) and cf. *Canarium* sp. ('kekuna' nut).

Charred fragments of fruit exocarp comprising distinctive roundish to polygonal nodules or disks, *ca.* 1-2mm in size, with a small central perforation were identified in all five Pleistocene contexts analysed. Based on published descriptions including of previously identified archaeobotanical material from Holocene contexts at Kitulgala, these are tentatively

641 identified as breadfruit (*Artocarpus* sp.) skin. Fissuring of the nodules is consistent with the
642 fracture patterns observed in experimentally cooked and charred breadfruit cultivars in
643 Oceania (Kahn and Ragone 2013), suggesting the charred Kitulgala fragments were also
644 produced by roasting, though additional experiments with Sri Lankan wild varieties is needed
645 to replicate these observations. In addition, a single fragment of cf. *Canarium* sp. endocarp
646 (nutshell) was identified in Context 10. The fragment was <3mm in size and identified
647 tentatively based on the presence of a distinctive cellular pattern observed on the inner seed
648 locule (Fairbairn pers. comm. 2018). Additional comparative work with modern reference
649 material is needed to confirm this identification. Other nutshell fragments were also observed
650 in other contexts but these have not yet been identified.

651 The presence of cf. *Artocarpus* sp. and cf. *Canarium* sp. in the archaeobotanical assemblages
652 is consistent with a rainforest plant food economy being practised at Kitulgala throughout the
653 Late Pleistocene, as also observed at other rockshelter sites in the Wet Zone (Perera et al.
654 2011; Kajale 1988). Previous archaeobotanical studies at Kitulgala also identified charred
655 breadfruit and *Canarium* remains, as well as wild banana (*Musa* sp.) in Holocene deposits
656 dating to at least 12,500 BP. Whilst additional work is needed to confirm the identifications of
657 the new Kitulgala samples, the present study tentatively extends the chronology of the
658 rainforest subsistence economy into the Pleistocene. Furthermore, it indicates that at least
659 wild breadfruit was probably exploited from initial occupation of the site at around 44,000
660 years ago. Wild breadfruit (*Artocarpus nobilis*) and kekuna nut (*Canarium zeylanicum*) are
661 both endemic to Sri Lanka and grow today in the lowland rainforest (Gunatilleke et al. 2008).
662 Together these provide a rich source of starch, fats and protein, and require little processing
663 other than cooking (in the case of breadfruit), making them high ranked food resources. The
664 storability and transportability of *Canarium* nuts would have made them an attractive resource
665 for a mobile hunter-gatherer population.

4.6 Lithic Technology

The lithic assemblage of Kitulgala Beli-lena comprised of 15,151 lithic items and 33 quartz pebbles, probably utilized as hammerstones (Table 8). The main raw material used was quartz, with small numbers of chert artefacts identified, including four flakes and one fragment in the Holocene, five flakes, two chips and one core-on-flake in the Terminal Pleistocene, and three flakes and three fragments in the Late Pleistocene. Small and medium size quartz pebbles can be found in immediate vicinity of the site, including in the nearby stream and in open sedimentary sections. The primary source of chert is unresolved, and likely represents elements of toolkits that have been transported to the site.

The technological reconstruction of the lithic *chaîne opératoire* indicates the continuous use of the bipolar-on-anvil method from the Late Pleistocene to the Holocene. The cores are characterized by the typical battering marks of the hammerstones on the proximal end and by small breakages produced by the contact with the anvil. Generally, the quartz pebbles were exploited along their longer axis in order to maximize the length of the by-products. At times, during the knapping events, the striking platforms were shifted in order to achieve a better stability on the anvil. This behaviour is common in the different chronological phases and several examples document the opportunistic use of striking platforms opposed to flat surfaces, natural or created during the reductions (Figure 6, 2-3), and the rotations of the cores of 90° degrees (Figure 6, 1), producing flakes with orthogonal scars on the dorsal surfaces.

The flake assemblage is composed mostly of fragments and small chips whereas complete flakes and flake bladelets are recorded in lower frequencies (Table 9, Figure 6, 4-8). Comparison of unbroken flakes by length intervals indicates that the knapping events were aimed to produce small blanks with the size of most of the artefacts smaller than 30 mm (Figure 7). However, some slight changes through time were documented. From the Late Pleistocene, there was a decrease in the frequency of flakes smaller than 20 mm and an

increase in the frequency of artefacts in the intervals of 30 - 40 mm (Figure 7). Since during the bipolar-on-anvil reduction, the size of knapping by-products is not controlled as in other hierarchical technologies (Picin and Vaquero, 2016; Boëda, 2013), the greater number of larger flakes during the Terminal Pleistocene and Holocene could be linked to the gathering of bigger quartz nodules or the exploitation of different secondary outcrops where larger cobbles were available. Typical by-products of the bipolar-on-anvil reduction sequences are few in the flake assemblage. Siret knapping accidents represent 10.5% of the fragments from the Late Pleistocene, 8.4% from the Terminal Pleistocene and 7.1% from the Holocene. Conversely, splinter piece total only 32 blanks in Late Pleistocene, 33 blanks in the Terminal Pleistocene and 25 blanks in the Holocene.

Table 8. Total number and percentage of the lithic assemblages of Kitulgala Beli-lena by chronological phases.

Phase	Flake	Flake Bladelet	Fragment	Debris	Core	Core Frag.	Hammer	Total
Holocene	523	9	2367	620	43	34	7	3603
%	14.5	0.2	65.7	17.2	1.2	0.9	0.2	100
Terminal Pleistocene	592	1	2635	3230	68	45	6	6577
%	9	0	40.1	49.1	1	0.7	0.1	100
Late Pleistocene	544	2	2324	1998	57	67	20	5012
%	10.9	0	46.4	39.4	1.1	1.3	0.4	100
Total	1659	12	7326	5848	168	146	33	15192
%	10.9	0.1	48.2	38.5	1.1	1	0.2	100

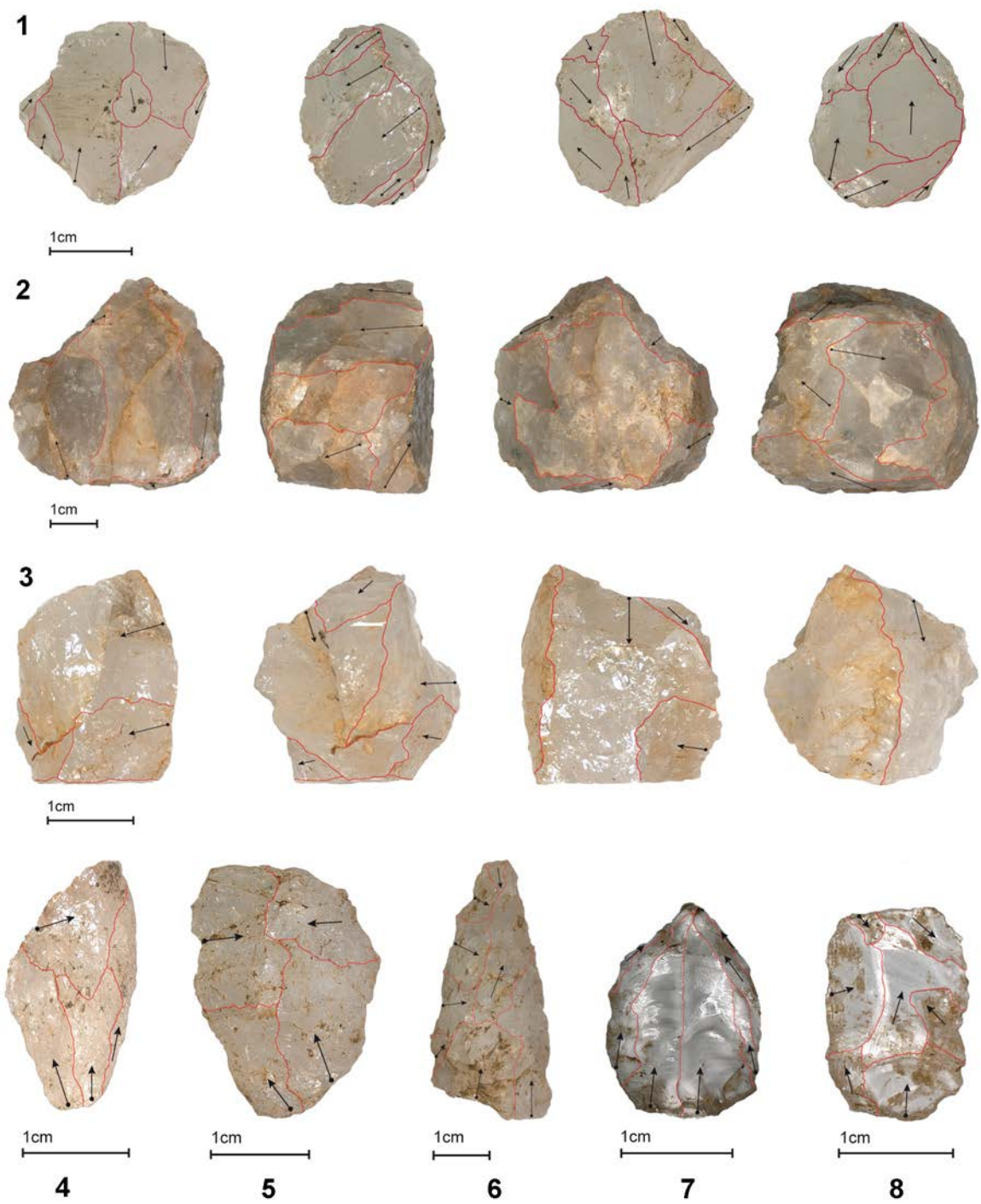


Figure 6. Bipolar-on-anvil cores (1 – Holocene; 2 – Terminal Pleistocene; 3 Late Pleistocene) and bipolar flakes (4, 5 – Holocene; 6 – Terminal Pleistocene; 7-8 Late Pleistocene) from Kitulgala Beli-lena.

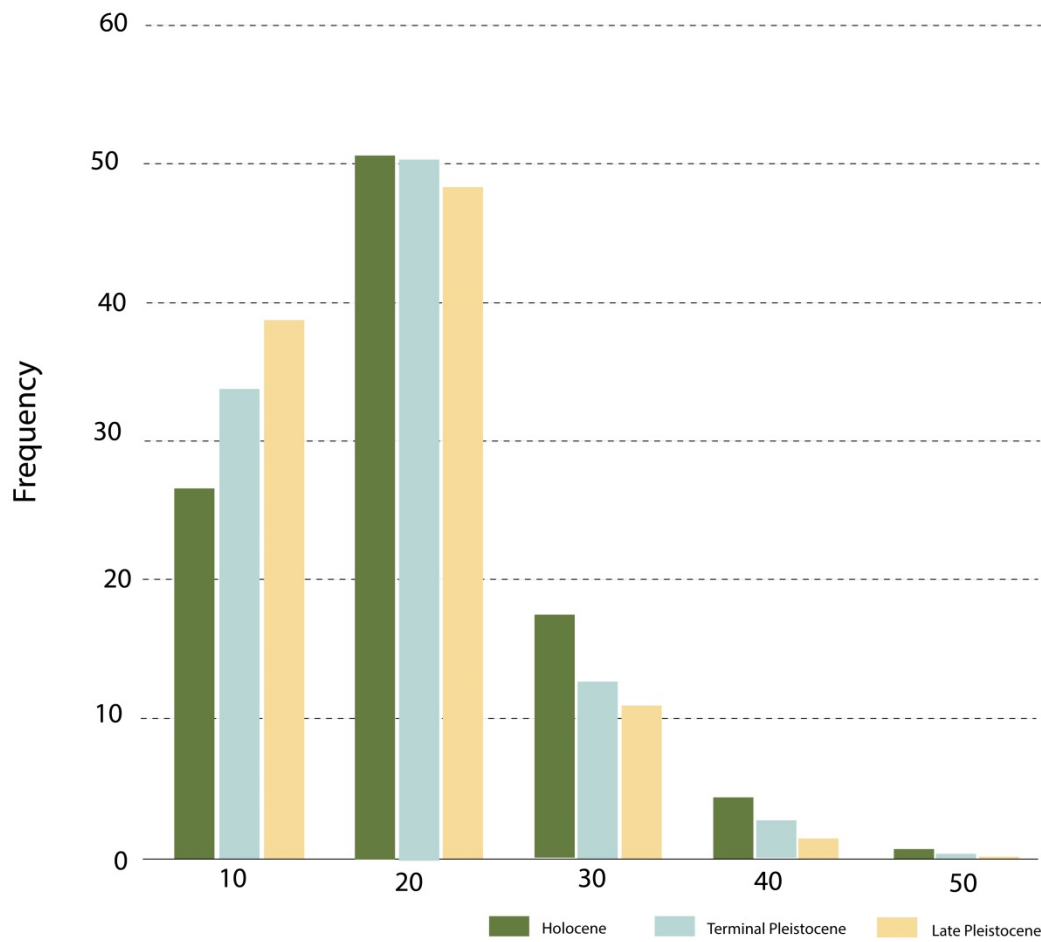


Figure 7. Histogram of the frequency of complete flakes by length intervals during the different chronological phases at Kitulgala Beli-lena.

Although they were documented, albeit in low frequencies, in previous fieldwork and analyses (Roberts et al., 2015a; Lewis, 2017), retouched tools and backed microliths are absent in the lithic assemblage analysed. From the 24,772 artefacts and more than 500,000 pieces of debris recorded in previous excavations, only 28 were identified as retouched tools. The technological continuity recorded at Kitulgala Beli-lena is in accordance with the evidence documented in other cave sites located in the modern Wet Zone rainforest of Sri Lanka. At Fa Hien-lena Cave, the lithic production was aimed at small blanks, and the bipolar-on-anvil method on quartz, with the expedient technique of rotating the core and

changing the striking platform, was used from ~48-45 ka up to the Holocene (Wedage et al., 2019a; 2019b). At Batadomba-lena Cave, bipolar cores were found in association with freehand flake and bladelet cores along with numerous backed microliths, a type of artefact that is not generally found in the other two sites (Lewis, 2017).

5. Discussion

Human behaviour and adaptations at Kitulgala Beli-lena

Our data provide new insights into the foraging strategies and material culture of human populations living at the site of Kitulgala Beli-lena. Firstly, our new radiocarbon dating programme has dramatically revised the dates for the site, making it now one of the oldest dated rockshelter/cave sites in Sri Lanka, and indeed South Asia more broadly. Indeed, the earliest occupation date of 44,000 cal. years BP places it approximately contemporaneous to Fa Hien-lena Cave and now earlier than the 38,000-36,000 cal. years BP recorded for Batadomba-lena (Perera et al., 2011; Roberts et al., 2015a). This re-dating emphasises the importance of applying robust pre-treatment methodologies in the tropics (as also highlighted by Higham et al. (2008) for the Niah Caves, Borneo), in order to avoid erroneously young dates as a result of detrital contamination. In the context of charcoal, this involves the application of the Acid Base Oxidation (ABOX) pre-treatment steps (Higham et al., 2008). Moreover, the re-dating of Kitulgala Beli-lena confirm the early presence of humans in the Wet Zone rainforests of Sri Lanka as early as *ca.* 45,000 years ago, an assertion that was previously solely based on the record at Fa Hien-lena (see also Wedage et al., 2019a).

The multidisciplinary approach presented here also enables us to confirm that this early record of human presence at Kitulgala Beli-lena is associated with clear evidence for rainforest foraging throughout the sequence. Archaeobotanical evidence from the Late Pleistocene and Holocene levels demonstrates the continued extraction and use of wild

breadfruit (*Artocarpus nobilis*) and kekuna nut (*Canarium zeylanicum*) by foragers at the site. Both of these plants provide a rich source of starch, fats, and protein, and require little processing. This makes them highly productive food resources in an environment that has often been considered to lack reliable plant-based sources of carbohydrate and protein (Bailey et al., 1989; Gamble, 1993). *Canarium* sp. nuts have also been documented at Fa Hien-lena and Batadomba-lena (Perera et al., 2011; Wedage et al., 2019a), as well as Late Pleistocene sites in Southeast Asia and New Guinea (Summerhayes et al., 2010; Barker and Farr, 2013), highlighting their potential significance to early human tropical foragers in these parts of the world.

Zooarchaeological and taphonomic insights from the Holocene layers (8,029-10,577 cal. BP) of Kitulgala Beli-lena further support a specialized rainforest exploitation and use of small mammals, primarily semi-arboreal and arboreal primates and squirrels, that has been documented with striking similarities at Late Pleistocene and Holocene levels at Fa Hien-lena and Batadomba-lena. Wijeyapala (1997) reported the presence of animal bones in the Pleistocene layers of Kitulgala during his excavation of the outer, eastern section of the rockshelter. Although no systematic zooarchaeological analyses were conducted, he noted the presence of cercopithecoid bone fragments in the site's lower sediment layers. Interestingly, however, faunal remains were not recorded from the Pleistocene levels during the 2017 excavations of the inner western section of Kitulgala Beli-lena. The absence of any animal skeletal or dental remains was also noted in the sediment micromorphological analysis conducted by Kourampas et al. (2009). This seemingly indicates that animal butchery and processing was done in different parts of the site during the Pleistocene.

The osseous and lithic technological remains recovered from Kitulgala Beli-lena further confirm evidence from Fa Hien-lena that Late Pleistocene and Holocene foragers in Sri Lanka had developed a sophisticated repertoire for the exploitation of their immediate landscapes.

788 Osseous tools were found within the Holocene levels of Kitulgala Beli-lena, including
789 finished unipoints, bipoints and geometrics. The bone points were most likely utilized as
790 projectile points similar to those found in Fa Hien-lena (Wedage et al., 2019a; Langley et al.,
791 2019). The lithic materials, while not representing any backed microliths, show a bipolar-on-
792 anvil reduction method on quartz with stark similarities to those seen at Fa Hien-lena and
793 Batadomba-lena where microlithic points appear to have been the final goal (Lewis et al.,
794 2014; Lewis, 2017; Wedage et al., 2019a; 2019b). The absence of retouched tools and backed
795 flakes in this area of the site may indicate that tool-use occurred in a different part of the
796 rockshelter or at another location altogether. Since faunal remains were recorded previously
797 in the Pleistocene deposits (Wijeyapala, 1997) and they are lacking in the area excavated in
798 2017, it is probably that butchering activities, microlith preparation, and gear retooling were
799 carried out in specific tasks locations of the rockshelter. This different spatial distribution of
800 the remains suggests a complex organization of the site that is common in prolonged (long-
801 term) settlements (Bartram et al., 1991; O'Connell et al., 1991). This, alongside the lack of
802 bone tools and faunal remains from the Late Pleistocene layers, supports the differential use
803 of space by Late Pleistocene and Holocene foragers at Kitulgala Beli-lena.

804 Recent analysis of the lithic assemblages of the previous excavations recorded the presence of
805 27 microliths in the Late Pleistocene, and four in the terminal Pleistocene. Similarly, where
806 bone tools are present in Holocene levels, there is no *débitage* evidence implying that they
807 were manufactured elsewhere. As a result, while material culture and archaeobotanical and
808 zooarchaeological evidence at Kitulgala Beli-lena, and its neighbouring sites, demonstrates a
809 well-tuned, persistence foraging adaptation to the rainforest environments of Sri Lanka, there
810 appears to be spatial complexity into how this adaptation was practised on a site and
811 landscape basis, represented within a given site, in a given period, and, indeed, perhaps across
812 the landscape. Given that systematic lithic, material culture, and subsistence analysis has now

taken place at Fa Hien-lena (Deraniyagala, 1992; Roberts et al., 2015b; Wedage et al., 2019a,b), Batadomba-lena (Perera, 2010; Perera et al., 2011; Roberts et al., 2017a), and, here, Kitulgala Beli-lena (sites that lie within 100km² radius of each other in the Wet Zone evergreen rainforests), future, systematic comparative work promises to further enrich understandings of the spatial organisation of tropical rainforest use by Late Pleistocene and Holocene hunter-gatherers on the island of Sri Lanka.

Kitulgala Beli-lena in context - Late Pleistocene-Holocene rainforest foraging and its social context in Sri Lanka and South Asia

The multidisciplinary evidence from Kitulgala Beli-lena, Fa Hien-lena, and Batadomba-lena now demonstrates the persistent use of tropical rainforest resources from 48,000-45,000 years ago through to 3,000 years ago in the Wet Zone of Sri Lanka (Wedage et al., 2019a). Stable isotope evidence from human and animal tooth enamel from Batadomba-lena, Fa Hien-lena, and Balangoda Kuragala demonstrates that between 36,000 and 3,000 years ago human foragers were reliant on tropical rainforest resources year round (Roberts et al., 2015a, 2017b), while detailed zooarchaeological and archaeobotanical information demonstrates that this lifestyle was supported by a heavy focus on semi-arboreal and arboreal primates and tree products and supplemented by freshwater molluscs and squirrel taxa (Perera et al., 2011; Wedage et al., 2019a). This research, as well as finds in East Africa, Southeast Asia, and Melanesia (Barker et al., 2007; Summerhayes et al., 2016; Shipton et al., 2018) has gone a significant way to rehabilitating tropical rainforests as key habitats for *Homo sapiens* during its dispersal within and beyond Africa - environments that were once considered barriers to human dispersal (Gamble, 1993; Bird et al., 2005; Boivin et al., 2013). The scale and intensity of rainforest occupation and exploitation in Sri Lanka during the Late Pleistocene remains to be fully elucidated. Although one could argue that this occupation is characterized by highly-

838 mobile and low density human populations, growing evidence, including from stable isotope
839 analyses (Roberts et al., 2017a), as well as intense evidence of occupation of rockshelter and
840 cave sites (Perera et al., 2011; Wedage et al., 2019a; 2019b), suggests the persistent presence
841 of groups fully adapted to the dynamics of a rainforest environment.

842 Such a specialized adaptation is supported by evidence reported here from Kitulgala Beli-lena
843 that tool production and faunal butchery may have taken place across a wider social and
844 economic landscape in the Wet Zone rainforests of Sri Lanka. It is possible that Kitulgala
845 Beli-lena, Fa Hien-lena, and Batadomba-lena all formed part of a network of hunting ranges,
846 plant exploitation routes, and settlement strategies that were likely also augmented by open-
847 air sites that may never be discovered (see Mercader et al., 2003 for pessimism in this regard
848 in the Central African rainforest). Such a network between different groups, potentially
849 operating simultaneously, is also supported by growing evidence for contact between foraging
850 communities in the rainforest and populations on the coast. Evidence for marine shell beads
851 and shark teeth has emerged in the Pleistocene and Holocene levels of Fa Hien-lena and
852 Batadomba-lena (Perera, 2010; Perera et al., 2011; Langley et al., 2019), as well as the Dry
853 Zone site of Bellan-bandī Palassa (Perera, 2010). These items were most likely obtained by
854 trade with groups present in Sri Lanka's southern coast, identified in sites such as Bundala,
855 Patirajawela and Miniagalkanda (Deraniyagala, 1992), given that isotopic evidence points to
856 year-round reliance to rainforest resources by communities in the island's Wet Zone (Roberts
857 et al., 2015a, 2017a). As a result, it seems that the Wet Zone rainforests were home to an
858 established population that was part of wider social and symbolic networks with groups living
859 in other Sri Lankan biomes, not only on the coast but potentially also in the drier north and
860 south-eastern reaches given the lack of Pleistocene investigation of these regions to-date
861 (Deraniyagala, 1992; Roberts et al., 2015b).

Intriguingly, the basic lithic assemblage of bipolar flaked cores on quartz documented at the early rainforest sites in Sri Lanka, persists at postulated coastal sites, as well as at a number of Holocene hunter-gatherer sites (Roberts et al., 2015b). This includes the rockshelter site of Balangoda Kuragala in the Intermediate Zone, Bellan-bandī Palassa in the Dry Zone, a series of ‘Microlithic’ shell middens sites and, indeed, underlying contexts at the later Iron Age and urban site of Anuradhapura (Deraniyagala, 1992, 1997; Perera, 2010). Bone tools, supposedly of a similar nature to those found in the Wet Zone, have also been documented at Bellan-bandī Palassa (Perera, 2010). On top of isotopic evidence for the persistence of rainforest reliance at Batadomba-lena and Fa Hien-lena until 3,000 years ago and the arrival of the Iron Age in this part of the island (Roberts et al., 2015a), it therefore appears that human groups using similar technological repertoires persisted in the different biomes of Sri Lanka throughout the Late Pleistocene and into the Early and Mid-Holocene. Moreover, these groups apparently remained connected by exchange, and perhaps cultural affinities, throughout this period. Exploration of the scale and demography of these populations will require future work in different parts of the island. However, it seems reasonable to assume that the Wet Zone foragers were not isolated, mobile populations leaving ephemeral traces on their environment. Rather, their ability to persist in these settings, and not hunt primate populations to extinction, implies a certain sustainability of rainforest resource exploitation, perhaps in the form of spatial variation in hunting routes during different times of year or variation in targeted taxa (Roberts, 2016).

A Wider South Asian and Asian Perspective

From earlier assumptions of a rapid coastal arrival in South Asia *ca.* 60 ka (Mellars, 2005, 2006; Field et al., 2007), pictures of the appearance of our species in this part of the world have become much more complex over the course of the last decade (Groucutt et al. 2015;

Blinkhorn & Petraglia 2017; Roberts et al., 2017a). Significantly, given the data available from Kitulgala Beli-lena and the other Wet Zone sites of Sri Lanka, it is now clear that *H. sapiens* occupied and utilized a diversity of terrestrial environments, away from the coast, from its earliest arrival in South Asia. This includes the arid environments of the Thar Desert, from potentially as early as *ca.* 114 ka, perhaps supported by increased precipitation and the freshwater of palaeochannels and lakes (Blinkhorn et al., 2013, 2017, 2019). The Jurreru River Valley has also provided evidence for human populations in mosaic of dry forest, grassland, and riparian habitats, with fluctuating periods of aridity from 77 ka through to the Holocene (Petraglia et al., 2007; 2010, 2012; Clarkson et al., 2012). It is perhaps in Sri Lanka, however, that human adaptability to different extremes is most evident in South Asia. Here, sites producing the earliest current evidence for human fossils in the entirety of South Asia, as well as long-term records of human behaviour, are associated with specialized adaptations to tropical rainforest environments from 48-45,000 years ago through to 3,000 years ago. While this is not to say that coasts were irrelevant to late Pleistocene human occupations in this part of the world (Blinkhorn et al. 2017, 2019), and indeed future work on Sri Lankan coastal sites is likely to reveal prehistoric settlements in these parts of the island as well (Deraniyagala, 1992). It is now clear that the peopling of South Asia was far more complex than a coastal highway that rapidly brought uniform populations and technological strategies throughout this diverse region.

Research in South Asia over the past two decades points to a complex pattern of cultural and technological change following the initial *H. sapiens* colonization of the region. In western India, the Son Valley of north-central India and in the Jurreru Valley of southern India, it has been argued that Late Palaeolithic and microlithic toolkits transitioned from Middle Palaeolithic technologies (Sali 1989, Clarkson et al., 2009; Petraglia et al., 2012; Blinkhorn

2018; Clarkson et al. 2018). This can be clearly seen in the Jurreu Valley, where Middle Palaeolithic occupations span 77-38ka, with the younger assemblages sharing features that become central to subsequent Late Palaeolithic industries from 35ka onwards (Petraglia et al., 2007; Clarkson et al. 2012). It also appears that microlithic and osseous tool technologies were utilized by communities occupying a diverse range of terrestrial environments far from the South Asian coast. Bone tools were recorded in the Jwalapuram Locality 9 site alongside Late Palaeolithic stone tools (Clarkson et al., 2009). Likewise, bone technology including projectile points presumed to have been utilized to hunt arboreal fauna, alongside quartz microliths, have been recorded in the earliest phase of occupation of the rock shelter sites in Sri Lanka's Wet Zone region (Deraniyagala, 1992; Perera, 2010; Perera et al., 2011; Wedage et al., 2019a; Langley et al., 2019). The sophisticated microlithic and osseous technologies, as well as ochre and symbolic beads, documented in these sites would not be out of place in the caves of western Europe 45,000 years ago (Conard, 2010) or in southern Africa from 100,000 years ago (Henshilwood et al., 2011), perhaps causing us to reorient our ideas of which ecological adaptations accompany symbolic, technological, and economic hallmarks of our species.

Evidence for Late Pleistocene rainforest occupation and resource utilization, akin to evidence from Sri Lanka's Wet Zone sites, has also been documented in Southeast Asia and Melanesia. The most comprehensive evidence for Late Pleistocene rainforest subsistence foraging strategies in the region comes from Niah Caves in Sarawak, Borneo. Niah Caves produced one of the earliest human fossils in Southeast Asia, dated to c. 44,000–40,000 cal. years BP (Barker et al., 2007; Higham et al., 2008; Reynolds and Barker, 2015). Results of detailed analyses looking at a wide range of archaeological materials including fauna, pollen, pytholiths, starch grains, and macrobotanical remains, point to complex foraging behaviours tailored to take full advantage of the rainforest environment (Barker and Farr, 2016). These

937 include exploitation of an array of plant resources for food and possibly clothing, processing
 938 of toxic plants such as taros and yams, specialized targeting of wild boar, hunting of arboreal
 939 taxa including monkeys and civet cats, as well as collection and processing of freshwater
 940 molluscs (Barker et al., 2007; Barton et al., 2009; Barton, 2016; Hunt et al., 2012; Piper and
 941 Rabett, 2014; 2016; Szabó, 2016). These activities were facilitated by some of the earliest
 942 bone tools found in Southeast Asia (Rabett and Piper, 2012; Rabett, 2016) in addition to flake
 943 based stone tool technologies (Reynolds, 2016; Barton, 2016). The earliest human occupation
 944 of Melanesia is also associated with rainforest foraging. Sites in the Ivane Valley region of
 945 Papua New Guinea produced evidence for processing of *Dioscorea* yams and *Pandanus* nuts
 946 as early as 49,000–43,000 cal. years BP (Summerhayes et al., 2010). Human occupation of
 947 rainforests have also been recorded in the Bismarck Archipelago at sites in New Ireland dated
 948 to c. 40,000 cal. years BP (Leavesley, 2005) and in West New Britain c. 35,000 cal. years BP
 949 (Pavlides, 2004; Summerhayes et al., 2017).

950 It is now becoming increasingly apparent that what truly characterises our species is its
 951 emergence at a time of increasing climatic and environmental variability in Africa (Potts et
 952 al., 2019). Not only did this act as the background for the evolution of diverse human
 953 populations in different parts of this continent (Scerri et al., 2016), but it is also the situation
 954 that met members of *H. sapiens* moving into Europe, Asia, Australasia, and the Americas
 955 during the Late Pleistocene (Roberts and Stewart, 2018). While in some cases coastal
 956 environments or savannah settings may have been significant to human populations utilizing
 957 new projectile technologies, and developing novel symbolic networks (Shea, 2011; Marean,
 958 2016), these behaviours also supported the movement of populations into more ‘extreme’
 959 environments including high-altitude settings (Stewart et al., 2016), desert settings (Hiscock
 960 and Wallis, 2005; Nash et al., 2016), the arctic (Pitulko et al., 2016), and tropical rainforests
 961 (Barker et al., 2007; Roberts and Petraglia, 2015; Roberts et al., 2017a; Westaway et al.,

2017). While research focus on these latter environments has been largely lacking in contrast to temperate and grassland parts of Europe and Africa, two decades of research has revealed a vast wealth of information into human subsistence, technological adaptations, and symbolic behaviours (Aubert et al., 2014; 2018; Langley et al., 2019). Increased multidisciplinary excavation, and analysis in parts of the world dominated by these more ‘extreme’ habitats in the present, as well as the past, has the possibility to enable us to build a more complete picture of the ecological and social adaptations that make us human, and enabled us to colonize nearly the entirety of the planet by the end of the Pleistocene.

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Discussion

This project has focused on reconstructing the Late Pleistocene and early Holocene prehistory of Sri Lanka in more detail than ever before. In doing so, it has focused on the unique specialized adaptations of *Homo sapiens* to the Wet Zone lowland rainforests of the island represented by key cave and rockshelter sites. The natural vegetation of this ecozone (D1) comprises equatorial rainforest (for eco-zoning ref. Deraniyagala 1992: app. I), an environmental context previously considered to have been unattractive for human forager occupation (Bailey et al., 1989; Gamble, 1993; Bird et al., 2005). Research into Wet Zone cave and rockshelter deposits has accelerated during the last three decades from slow, rudimentary beginnings in 1978 at Kitulgala Beli-lena (ibid.; Wijeyapala 1997), at Batadomba-lena (Deraniyagala 1992; Perera 2010) and finally at Fa Hien cave (Deraniyagala 1992; Wijeyapala 1997), all situated within c. 35 km from each other. A literature survey of the above indicates that while these investigations were sound, particularly those of Perera (2010) at Batadomba-lena, the resultant data density was far from adequate as a basis for more reliable interpretations. The most evident shortcomings pertained to (a) chronological uncertainties linked to a lack of radiocarbon dating approaches using the most recent pretreatment techniques and modeling; b) a lack of palaeoenvironmental data particularly prior to c. 15,000 BP; (c) limited, detailed understanding of settlement and subsistence and the foraging and hunting techniques that supported specialized tropical rainforest reliance and, finally; d) uncertainty as to how enigmatic microlith technologies in the region were used in rainforest adaptations across space and time. With the exception of Batadomba-lena (Perera 2010; Perera et al. 2011; Lewis et al. 2014) little was known about these technologies and their role in facilitating exploitation of the lowland Wet Zone tropical forests.

To resolve the above-mentioned research questions, this thesis intensively investigated two of the most promising sites, Fa Hien-lena and Kitulgala Beli-lena, employing state-of-the-art and multidisciplinary sampling and post-excavation analytical techniques that had previously been only sparingly applied at the site of Batadomba-lena (Perera et al., 2011). The excavations and post-excavation analyses succeeded in adding a substantial corpus of data to those already at hand, yielding new high-resolution insights into the timing of human arrival in the Wet Zone rainforest of Sri Lanka, the fauna and plant resources that human populations procured from 45,000-3,000 years ago in these settings, and the technological adaptations that enabled them to do so. These novel findings are hereby synthesized in order, prior to a final comment on the significance of Late Pleistocene archaeology in Sri Lanka for understanding the arrival and expansion of our species in South Asia and Asia more widely.

Chronology

The previous age-range for Kitulgala Beli-lena was over 31,000 - 3500 cal BP (Deraniyagala 1992; Wijeyapala 1997), while the previous range of human occupation for Fa Hien-lena was 32000 – 4000 cal BP (Deraniyagala 1992; Wijeyapala 1997). However, in the last two decades it has become apparent that without robust pretreatment of charcoal samples used for radiocarbon dating, the produced ages are frequently ‘too young’ in tropical contexts (Higham et al., 2007). Indeed, this was confirmed by the re-dating of these two sites performed in this thesis, which demonstrated the earliest period of human occupation of Kitulgala Beli-lena to be c. 44,000 cal BP (Wedage et al. submitted) and that of Fa Hien-Lena to be 48,000 cal BP (Wedage et al., 2019a). This dramatically alters our understanding of human activities at these sites as well as the tempo of the occupation of Sri Lanka’s rainforest environments.

Firstly, it is now clear that humans were present in tropical rainforest environments in South Asia by at least 45,000 years ago, roughly the same time as the in-depth records of human use of tropical forest resources at the Niah Caves, Borneo (Barker et al., 2007; Barker and Farr, 2016) and the Ivane Valley, New Guinea (Summerhayes et al., 2010). Secondly, instead of this being represented by intermittent occupations of Fa Hien-lena, then Batadomba-lena, and Kitulgala Beli-lena it now appears that all three sites were occupied at the same time c. 45-38,000 years ago (Perera et al., 2011; Wedage et al., 2019a, submitted). Indeed, it is highly likely that re-dating of Batadomba-lena would lead to similar revisions in radiocarbon ages (Roberts et al. 2015b).

This new chronology not only makes the Sri Lankan Wet Zone rainforest one of the first tropical rainforests on the planet with clear and persistent evidence of human occupation, but also suggests that it represented a complex landscape of different foraging groups. Coincident occupation and use may be the product of different populations, or the same mobile population, leaving extensive traces through this portion of the Wet Zone. It is likely that we are missing a number of open-air sites that do not preserve well in these environments (Mercader et al., 2003), which would further contribute to our understanding of this inhabited environment. Given evidence for contact with coastal groups in the Late Pleistocene it also seems that there were extensive trading and communication networks in Sri Lanka at this time, something that may become even more apparent with future work in different parts of the island (Wedage et al., 2019a, submitted).

Settlement and subsistence

Currently, the new dates obtained for Fa Hien-Lena in this thesis (c. 48,000 cal BP), make it the oldest record of *Homo sapiens* in Sri Lanka (Wedage et al., 2019a). While there is tentative evidence for sites in the coastal dunes of Sri Lanka's Dry Zone that may precede this date (Deraniyagala, 1992), there is currently no reliable chronometric evidence available. As a consequence, this means that the earliest definitive records of human fossils and activity at Fa Hien-lena (48,000 years ago) and Kitulgala Beli-lena (44,000 years ago) suggest a tropical rainforest environment for the earliest occupants of Sri Lanka. These environments also appear to have supported *Homo sapiens* arriving in Southeast Asia between c. 70,000 and 45,000 years ago (e.g. Barker et al., 2007; Westaway et al., 2017 and in Melanesia 45,000 years ago (Summerhayes et al., 2010, 2016). As a result, in contrast to assumptions that humans would have avoided these environments in favour of grassland corridors or coastal 'highways' (Bird et al., 2005; Mellars, 2006), it seems that our species was capable of rapidly adapting to a diversity of tropical rainforest habitats during its expansion into these parts of the planet in the Late Pleistocene.

It should be noted that the archaeological record of Late Pleistocene Sri Lanka is biased towards the Wet Zone cave and rockshelter sites, as a product of research focus and the gneiss geology that is resistant to weathering. However, the available palaeoecological evidence uncovered from these sites for this thesis, coupled with other studies from the Sri Lankan wet zone, provides ample evidence that early *Homo sapiens* in this part of the world were particularly tuned towards rainforest foraging. These environments would have provided ample access to freshwater in the form of regular rain and the resulting streams, as indicated by freshwater molluscs analyzed at both Fa Hien-lena and Kitulgala Beli-lena as part of the work reported in this thesis (Wedage et

al., 2019a, submitted). There is no indication that conditions would ever have been notably arid, even during the Last Glacial maximum period, though there may have been alterations in forest cover and type during this time (Roberts et al., 2015a, 2017).

Large concentrations of terrestrial and freshwater molluscan remains have been reported from the Sri Lankan wet zone sites (Deraniyagala, 1992; Perera et al., 2011). Although quantitative data is largely absent from much of the published Sri Lankan literature (although see Perera et al., 2011; Wedage et al., submitted), the density of the invertebrate fauna led Deraniyagala (1992) to comment that molluscs must have constituted an important source of protein, forming one component of a broad-spectrum economic structure. The presence of *Acavus* spp. terrestrial and *Paludomus* spp. freshwater gastropods at Batadomba-lena has been interpreted as indicating consistent access to free-flowing freshwater conditions and continuity of rainforest conditions around the site (Perera et al. 2011). These authors did however report a shift from predominantly terrestrial to predominantly freshwater taxa after c. 16,000 BP, which may indicate a subtle environmental shift, or alternatively a change in foraging strategies around the site.

This pattern is supported to some degree through the recent analyses for this research of the Kitulgala Beli-lena assemblage, supplemented by a preliminary assessment of a small sample of invertebrates from Fa Hien-lena (Wedage et al., submitted). Whether the taxonomic shift post-LGM reflects a broader ecozone trend, or is restricted to Batadomba-lena remains to be determined, although the Kitulgala Beli-lena assemblage analysed, which is restricted to the Holocene, is dominated by the Paludomidae. Following the point raised by Deraniyagala (1992), the role of these resources within the overall dietary structure needs careful assessment through robust quantitative and taphonomic analyses.

The available archaeozoological and archaeobotanical data also points towards the clear ability of rainforest foragers to procure enough protein and carbohydrate resources in these environments. From at least 44,000 years ago there is clear evidence for the broad-spectrum exploitation of small arboreal and semi-arboreal mammals, such as cercopithecoid monkeys and giant squirrels, at the sites of Fa Hien-lena and Batadomba-lena (Perera et al., 2011; Wedage et al., 2019a). This prey would have been fast and difficult to catch, but nonetheless dominate the faunal assemblage throughout the Late Pleistocene and into the Holocene, as documented by Kitulgala Beli-lena (Wedage et al., submitted). The scarcity of larger animals, such as sambar or wild boar, reflects their frequency in the Wet Zone lowland rainforests of Sri Lanka today, though some larger animals, including rhinoceros, were encountered during the Holocene (Wedage et al., submitted).

It has been suggested that rainforest mammals, namely primates, are particularly vulnerable to human over-hunting (Mittermeier, 1987). However, ethnographic research has highlighted how modern hunting populations will focus on killing certain portions of the population, and even switch between sympatric species, in order to ensure a general ecosystem balance and ongoing availability of prey (Van Vliet et al., 2010). This is observable in the high-resolution zooarchaeological data from Fa Hien-lena where the targeting of mature arboreal monkeys, instead of juveniles, and the consistent exploitation of different primate species seems to have enabled the sustainability of this rainforest adaptation (Wedage et al., 2019a; see also Roberts, 2016) and the survival of these primate populations until the present.

Interestingly, some of the faunal identifications suggest that the Wet Zone forest environments may have been slightly different in the past to today. *A Axis* spotted deer and the grey langur are not present in the Wet Zone of Sri Lanka today, and instead characterize the Dry and

Intermediate Zones of the island. Nevertheless they occur in the Fa Hien-lena zooarchaeological dataset with the grey langur being present from 48,000 to 4,000 cal. years BP and the spotted deer in deposits dated to 12,000 to 4,000 cal. Years BP. In addition, stable carbon and oxygen isotope analysis of humans and animals from Batadomba-lena suggest that, between 36,000 and 20,000 cal. years BP, the tropical forests located in the Wet Zone may have been more similar to those found in the Intermediate Zone of the island today (Roberts et al., 2017). This is in keeping with suggestions that South Asian environments between 28,000-16,000 years ago were markedly drier than today. If this is the case then human populations may have been presented with more open forests and a higher degree of exploitable faunal and floral resources (Deraniyagala, 1992). This may have, in turn, resulted in higher carrying capacities for tropical rainforests in the region than often assumed. However, it should also be noted that the earliest human sampled for stable isotope analysis (36,000 years ago at Batadomba-lena) shows full reliance on closed, rather than open, rainforest resources (Roberts et al., 2017).

While the sophisticated exploitation of these different arboreal and semi-arboreal fauna is of major significance, it is also clear that the exploitation of tropical rainforest food plants would have played an integral role in the subsistence strategies of hunter-gatherers in the wet tropics. However, there has been limited systematic specialist investigation of the plants exploited in Late Pleistocene Sri Lanka. The meagre data from the three cave/rockshelter sites to have survived the ravages of their wet equatorial environment indicate the persistent exploitation of wild breadfruit, wild banana, and canarium nuts (Perera et al., 2011), including from first occupation of Kitulgala at *c.* 45,000 cal BP (Wedage et al., 2019a; submitted), though their overall economic role remains uncertain. Ethnographic analogues from the Wanniyalaeto (Veddah) groups of Sri Lanka suggest that the main calorific input would have been from the

collection of *Dioscorea* yams, perhaps supplemented by carbohydrates from starch extracted from wild toddy palms (*Caryota urens*) and sugar from bees' honey (Deraniyagala, 1992), as well as the economically significant trees noted above. Identification of the full spectrum of botanical resources exploited by Late Pleistocene humans in the Wet Zone of Sri Lanka awaits further pollen, phytolith, starch and macro-remain analyses.

Technology

As is invariably the case with prehistoric cultural deposits, the majority of artefacts recovered from the cave sites in the lowland Wet Zone of Sri Lanka is comprised of lithic material. Most organic remains would have been less resistant to chemical and physical weathering that is integral to this ecozone, though some osseous technologies have also been recorded (Wedage et al., 2019; Langley et al. submitted). Since the 1980s it was noted by Siran Deraniyagala (1992) that microlith stone tools appeared in Sri Lanka earlier they did in Europe. Nevertheless, systematic analyses of these quartz microliths has been limited beyond broad typological analysis (Deraniyagala, 1992; Wijeyapala, 1997; Perera, 2010), with the exception of one comparative study of Batadomba-lena (Lewis et al., 2014). In this thesis I sought to i) clarify the age of these microliths, and associated bone tool technologies, following on from the re-dating of sites above and ii) undertake a systematic, quantitative, and chaîne opératoire approach to the lithics and organic tools recovered from Fa Hien-lena and Kitulgala Beli-lena in order to facilitate more in-depth comparisons with materials from Pathirajawela, Bundala, Embilipitiya and Batadomba-lena (Deraniyagala 1992; Wijeyapala 1997; Perera 2010).

Microlith Technologies

The ‘Microlithic’ techno-phase of Sri Lanka is characterised by the occurrence of small (< 4 cm-long) backed flakes or bladelets. In Sri Lanka, the earliest dated deposits with microliths have been found at Fa Hien-lena (c. 48-45, 000 cal BP). This site, dated by the present project, served to confirm and extend back the Batadomba-lena dates (c. 38/36, 000 – 12, 000 cal BP) (Perera et al., 2011; Roberts et al., 2015a), while direct re-dating of the microlith-bearing dune sands at Pathirajawela and Bundala (previously dated to c. 28 – 22, 000 TL BP) is currently in progress. These early dates for microliths are not as anomalous as previously thought, since, apart from the southern African microlithic industries dating to as far back as c. 80 ka BP (Brandt et al., 2012; Brown et al., 2012; Diez-Martín et al., 2009; Shipton et al., 2018; Wurz, 2013), comparable dates have now been obtained for microlithic industries in South Asia and beyond. A broad overview of the literature leads to the following dates for microlithic arrival in different parts of Asia, the Middle East, Africa, Europe, and Australasia:

- Central India, Narmada valley, open-air site, Mehtakeri, backed microliths, no geometric microliths: c. 45 ka (Mishra et al., 2013)
- Central India, open-air site, Patne, microliths: >25 ka (Clarkson et al., 2012)
- North India, middle Son valley, open-air site, Dhaba 3: c. 42 ka (Clarkson et al., 2018b)
- Eastern India, alluvial sediments, Kana, micro-blade reduction: c. 42 ka (Basak and Srivastava, 2017)
- Eastern India, alluvial sediments, Mahadebbra, geometric microliths: c. 36-25 ka (Basak et al., 2014)
- Western India, sand dunes, Buddha Pushkar, geometric microliths: >28 – 16 ka BP (Blinkhorn, 2018)

- Australia, Queensland and New South Wales, microliths: Late Pleistocene (Campbell, 1982; Hiscock and Attenbrow, 1998)
- South Africa, microliths: c. 71 ka BP (Brown et al., 2012)
- Tanzania, coast of Kenya, microliths: < 50 ka BP (Shipton et al., 2018)
- Levant, Ksar Akil and others, geometric microliths: c. 27 ka (Bergman et al., 2017)
- Central Asia, geometric microliths: c. 32 ka (Kolobova et al., 2018)
- Europe, Upper Palaeolithic, microliths: c. 45 ka (Benazzi et al., 2011; Sano et al., 2019)

Many of these microlithic industries are now thought to have developed locally from preceding autochthonous techno-traditions, such as the European Upper Palaeolithic and the Indian Middle Palaeolithic. Nonetheless, it is apparent, from the above chronology for the appearance of microliths on the world stage, that the appearance of lithic technologies targeting small blank sizes and backed geometric tools at Fa Hien-lena c. 48–45,000 cal BP, is some of the earliest evidence for microlithic technology outside of South Africa (Wedage et al., 2019b). Moreover, it is becoming apparent that the Sri Lankan microliths form part of a broader technological fluorescence across Asia and elsewhere in which *Homo sapiens* increasingly experimented with small stone tools as well as organic technologies (Petraglia et al., 2011), perhaps linked to growing populations and the need for flexible resource procurement in very different environments (Wedage et al., 2019b).

Based on the analysis undertaken in this thesis, and elsewhere, it is clear that a diverse range of local quartz material was exploited as the main raw material for producing small blanks at Fa Hien-lena, Kitulgala Beli-lena, and Batadomba-lena, , although chert is present at all three sites. At Fa Hien-lena, lithic technology appears to be nearly exclusively based upon bipolar flaking.

At Batadomba-lena, while bipolar cores constitute the most frequent single core type, the combined alternate types of freehand flake cores are more numerous than bipolar ones. Based on their small size it has been suggested that bipolar cores represent the final phase of core reduction before discard rather than an independent reduction strategy. Evidence for true bladelet production (fluted cores) is preserved at Batadomba-lena in just two specimens; however, it is absent in the area excavated at Fa Hien-lena. Finally, retouched artefacts are considerably more numerous in all levels of Batadomba-lena than at Fa Hien-lena, with numerous geometric microliths in association (Wedage et al., 2019b). The focus on bipolar technology in the earliest levels of Fa Hien-lena, to the exclusion of other reduction strategies, stands in contrast to the Late Pleistocene assemblages from Jwalapuram in South India where it is absent in the earliest Phase E, while appearing in low frequencies in the later phases D and C. It is noteworthy that bipolar technology has been observed in the Middle Palaeolithic assemblages in the immediate vicinity at Jwalapuram 20, 21 and 23 alongside sparse micro-blade-flakes ((Clarkson et al., 2018b; Petraglia et al., 2009)).

Long-term technological stability from the Late Pleistocene to the Early Holocene is a hallmark of the assemblages from all three cave/rockshelter sites investigated: Fa Hien-lena, Batadomba-lena and Kitulgala Beli-lena from 48, 000 to 4,000 BP (Lewis et al., 2014; Wedage et al., 2019a,b). Such stability has also been noted for the Hoabinhian techno-complex of the rainforests of tropical Southeast Asia (Forestier et al., 2013; Ji et al., 2016; Marwick, 2018). The available isochrons for the earliest appearance of microliths are centred around South Africa at c. 80 ka BP; whence they radiate into Eurasia by c. 45 ka BP ((Sano et al., 2019)). However, if this model is dismissed, as advocated by several eminent researchers, then the global emergence of microlithic technologies could be reconceptualised as result of technological convergence, rather

than the result of diffusion – be it direct diffusion or stimulus diffusion – from a single focus (Clarkson et al., 2018a). The diversity of environments in which microlithic technologies appear to have independently arisen is particularly striking in this regard (Wedage et al., 2019b). In this context Fa Hien-lena and Kitulgala Beli-lena document the earliest use of microlithic technologies in tropical rainforest habitats (Wedage et al., 2019b), suggesting that the use of this technology is not purely associated with the procurement of large mammals in grassland settings (e.g. Ambrose, 2002).

Osseous Technology

Osseous tools were found throughout the sequence at Fa Hien-lena (Wedage et al., 2019a) and Batadomba-lena (Perera et al., 2016) from 45 ka and 36 ka respectively onwards, while they and other osseous remains were absent from the Late Pleistocene layers of the area excavated at Kitulgala Beli-lena. These dates are comparable to the earliest dates for similar osseous artefacts from Niah Caves in Borneo (Barker et al., 2017), the Uluzzian layers of Grotta della Cala, Grotta del Cavallo and Grotta di Castelcivita in Southern Italy (d'Errico et al., 2012), and the Aurignacian layers of Mochi and Bombrini Shelters and Fumane Cave in the Italian Alps (Bertola et al., 2013). Analysis of the bone tools reveals that, in Sri Lanka, they were manufactured from cercopithecoid monkey long-bones by flaking, grinding and, at times, polishing, to produce small unipoints, bipoints, and geometrics (Perera et al., 2016; Wedage et al., 2019a). A single instance of the groove and splinter technique of blank excision from an antler was found from Fa Hien-lena from layer dated to 12,000 cal. years BP. A few of the unipoints and bipoints display incisions across their mid-section and a rare few are shouldered, probably to aid hafting. This evidence of hafting and the small lightweight size of the osseous

points suggest hafting onto wooden shafts as arrow-heads and that bow and arrow technology was employed (Wedage et al., 2019a). The geometrics do not display evidence of hafting. They may represent fishing gorges, or barbs within snares and netted traps for catching arboreal prey (Perera et al., 2016). There is some evidence to indicate that bone points increased in size during c. 45 ka of occupation at FaHien-lena, which appears to synchronise with an increase in size of prey hunted (Langley et al. submitted).

These bone technologies are the oldest identified in a tropical rainforest environment and systematic analysis of their parameters and *chaîne opératoire* provides some of the first clear, direct evidence that human populations in the Wet Zone of Sri Lanka employed bow and arrow technology to exploit the small arboreal and semi-arboreal fauna documented above (Wedage et al., 2019a,b). This is a major finding given that this kind of technology has often been associated with the reliable capture of ‘savannah’ game (e.g. Ambrose, 2002; Tryon et al., 2010) and highlights the flexibility this technological system offered our species as it advanced into a variety of environments within and beyond Africa during the Late Pleistocene (see also Shea and Sisk, 2010; Shea, 2011). Use-wear analysis has further demonstrated impact fractures on these tools (Langley et al. submitted). Moreover, the fact that these bone tools were made from monkeys and used to hunt monkeys also demonstrates the refined nature of this specialized rainforest adaptation. Beyond composite tools, this thesis has also identified large pieces of bone from cervids had been flaked in-to shape to resemble lithic cutting or scraping tools. Some of osseous artefacts display morphologies and wear consistent with use as awls (flaked monkey teeth), wedges (deer bones) and working of skins and plant fibres, which may represent the first evidence for clothing in a tropical rainforest setting.

Social and Symbolic Technologies

Beyond microliths and bone tool projectiles, this thesis has also advanced knowledge of symbolic material culture present in the Wet Zone rainforests of Sri Lanka during the Late Pleistocene. At Fa Hien-lena a spatula-shaped bone ellipse with nicks cut into its lateral edges was found at Fa Hien-lena from the Terminal Pleistocene occupational phase (12,500-8,000 cal. years BP). It is too thin to have served as a utilitarian tool and probably had a symbolic function. Two similar specimens had been excavated from Kitulgala Beli-lena in 1983 from a mixed context (Wedage et al. submitted). Abraded pieces of red and yellow ochre and graphite were found in Terminal Pleistocene layers of Fa Hien-lena. The graphite nodules had invariably been utilized to exhaustion, probably reflecting its scarce availability. It is noteworthy that some human remains, dated to 45ca 4ca, were found coated with red ochre at Fa Hien-lena (Langley et al. submitted).

Beads made of red ochre were found at Fa Hien-lena at layers dated to 8,700-8,000 cal. years BP. These red ochre beads show signs of anthropogenic perforation and polish suggesting that they transformed as pendant. Beads made on marine shells were found at Fa Hien-lena, Kitulgala Beli-lena and Batadomba-lena since the earliest settlements at 45 ka BP. These artefacts, common as *Homo sapiens* 's personal ornaments (Bar-Yosef Mayer et al., 2009; d'Errico et al., 2012), show one perforation and groove to facilitate suspension, and they are not colored with ochre. The sea coast is just at 80 km far from the Wet zone where the caves are located and the discovery of these marine shells could suggest the direct or indirect contact with groups living near the coast, keeping in mind that it is only c. 80 km distant from all three cave/rockshelter sites.

This ‘symbolic’ material culture has further enriched our understanding of social networks across Sri Lanka during the Late Pleistocene. Stable carbon and oxygen isotope evidence of human remains in the Wet Zone rainforests have indicated that humans were reliant on rainforest resources all year from from at least 36,000 years ago (Roberts et al., 2015a, 2017). As a result, it is highly unlikely that marine shells, as well as shark teeth noted elsewhere (Perera, 2010), were obtained through seasonal foraging rounds. Instead, it seems that different populations living on the coast, and perhaps within the rainforest, communicated with each other and exchanged material culture, potentially in order to buffer risk in both environments or to keep social relationships harmonious amongst rapidly growing populations across the island, as elsewhere in South Asia (Petraglia et al., 2011). Further investigation of Late Pleistocene sites on the Sri Lankan coast and in the Dry Zone of the island should further enrich our understanding of social and cultural interactions in the Late Pleistocene and Holocene.

Conclusion and Outlook

This thesis has made a major contribution to developing understandings of Late Pleistocene human colonization of the Wet Zone rainforests of Sri Lanka. Renewed excavation of two major cave sites, Fa Hien-lena and Kitulgala Beli-lena, have revolutionized our understanding of human arrival in South Asia’s tropical rainforests (Wedage et al., 2019a), pushing it back to 48,000 cal. BP. Moreover, it is now clear that three cave/rockshelter sites (Fa Hien-lena, Kitulgala Beli-lena, and Batadomba-lena) were occupied almost simultaneously during the Late Pleistocene, though Fa Hien-lena experiences a hiatus during the Last Glacial Maximum. This raises the possibility of studying landscapes of economic and cultural interaction in Sri Lanka’s

rainforests in the future and understanding how different populations within the rainforest moved and made use of different sites and resources (Wedage et al., 2019a, b).

The diverse multidisciplinary datasets reported here have also provided more in-depth understandings of the plant and animal resources targeted by rainforest foragers in Late Pleistocene Sri Lanka than ever before. This thesis has been able to document clear exploitation of small arboreal and semi-arboreal mammals at Fa Hien-lena (48,000-4,000 years ago) and Kitulgala Beli-lena (11,000 to 8,000 years ago) (Wedage et al., 2019a; Wedage et al., submitted). That this broad spectrum foraging emerged early on in the colonization of these extreme environments shifts narratives away from arguments that small mammal hunting was driven by demographic or climatic crises. Moreover, it is clear that human hunters in Sri Lanka had intimate ecological knowledge of their prey, monitoring age profiles and species in order to sustainably obtain protein resources into the Late Holocene (Wedage et al., 2019a). Supplemented with identified economic plants (e.g. *Canarium* sp., breadfruit), this reveals a rich profile of specialized rainforest foraging.

Finally, this thesis has also provided clear, systematic insights into the microlith and bone tool technologies associated with these adaptations. Not only has this work discovered the earliest microlith tools in a rainforest context anywhere in the world, but it has also revealed the first clear, direct evidence for bow and arrow use in Sri Lanka (Wedage et al., 2019a,b). Moreover, research into ochre and symbolic bone artefacts highlights the rich cultural and social network of Sri Lanka's Wet Zone, including the rich communication populations in this part of the island had with the coast (Wedage et al., submitted). Future work will focus on use-wear markers on microliths and more in-depth study of bead and awl technologies in order to provide further insights into how this material culture was created and used. Overall, however, this thesis has

enabled more comparative approaches to Sri Lankan prehistory, with technological, osseous, and symbolic material culture datasets on a par with Europe, Africa, and elsewhere in Asia (Wedage et al., 2019a,b; submitted) now available.

Compared to other parts of the world, notably Europe, with long-standing traditions of prehistoric archaeology, Late Pleistocene/Early Holocene investigations in Sri Lanka are still in their infancy. More archaeological and chronometric research is required on coastal sites where ‘Middle Palaeolithic’ technologies have been argued to underlie ‘microlith’ toolkits and potentially represent the earliest hominin occupation of the island (Deraniyagala, 1992). Survey in other parts of the Dry Zone is also required in order to determine whether the Wet Zone record is truly indicative of the onset of intensive human occupation in Sri Lanka. Further application of detailed zooarchaeological approaches, quantitative lithic comparisons, and stable isotope analysis of humans and fauna also hold much promise to determine how humans adapted to the different environments of Sri Lanka and what its impact was on different fauna. I hope to drive forward this work, through the multidisciplinary and multi-national collaborations that I have made during this thesis.

However, already the work presented here has turned Sri Lanka into one of the most significant regions of Late Pleistocene archaeological research in Asia at present. The datasets presented here represent one of the earliest clear records of human exploitation of rainforest environments anywhere in the world (Wedage et al., 2019a), with this region playing a major role in rehabilitation of these environments as key sites of human adaptation and expansion (see also Roberts and Petraglia, 2015). Moreover, Sri Lanka has produced some of the earliest microlith and bone tool records anywhere in Asia (Wedage et al., 2019a,b) firmly associated with an ‘extreme’ environment that has been frequently neglected in the context of human cultural

development. In doing so, Sri Lanka is now on a par with Borneo in Southeast Asia and New Guinea in Melanesia in revealing rich records of human interactions with tropical rainforest environments (Roberts and Petraglia, 2015; Roberts, 2019).

Indeed, Sri Lanka is now making major contributions to our understandings of the technological, cultural, and ecological capacities of our species more widely. It is becoming increasingly apparent that what defines our species, in contrast to other hominins, is its capacity to adapt to the whole diversity of environments that our planet has to offer. The colonization of deserts, high altitude environments, the palaeoarctic, and, in Sri Lanka, tropical rainforests began in earnest from the Late Pleistocene (Roberts and Stewart, 2018). Microlith and organic technologies, rather than being associated with coastal or ‘savannah’ resource use, were in fact part of a flexible package that enabled *Homo sapiens* to rapidly adapt to these diverse ecological situations. The work of this thesis, and that which is still going on in Sri Lanka, is driving some of these shifting perceptions, and will hopefully do so for many years to come.

References for Introduction and Discussion/Conclusion

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Appendices

Appendix 1. Further notes on stratigraphic phasing of Fa Hien Lena

Appendix 2. Further detail relating to analyses of faunal remains from Fa Hien Lena

Appendix 3. Lithic Materials from Fa Hien Lena

Supplementary References

Appendix 1. Further notes on stratigraphic phasing of Fa Hien Lena

The sediment fill of Fa-Hien Lena consists of ca. 170 cm of detrital sediment, representing at least 4 four major phases of occupation (Supplementary Figure 1) deposited above heavily weathered and karstified gneiss blocks, (phantomed bedrock and/or roof fall blocks) and steeply dipping, folded gneiss (Supplementary Figure 2-3).

Phase D: Late Pleistocene Occupation

Sediments directly above the gneiss slabs and bedrock comprise pebbly loams with angular spalls and sand, resulting from the disintegration of gneiss blocks, and clayey deposits which might have resulted from colluviation of soils/saprolith from outside. These sedimentary layers yielded faunal remains (28.7% of which showed evidence for burning and calcination), shell beads, ochre fragments, bone points, and quartz flakes, suggesting human presence in the cave. Above these facies is a ca. 30-50 cm thick succession of sharp-based, sub-horizontal layers of dark, sandy silt and laminated ash deposits that drape and interfinger with at least two distinct accumulations of angular gneiss blocks. These deposits are rich in charcoal and other organics and contain numerous faunal remains and artifacts.

Micromorphological analysis of four samples from Phase D deposits (corresponding to contexts 92, 91, 90; contexts 89, 88, 87; context 62 in the 2009 profile, Supplementary Figure 2) reveals various coarse grained microfacies with abundant and remarkably well preserved human occupation debris. Basal Phase D deposits consist of cm-scale beds and laminae of *in situ* phosphatised ash intercalated with gneiss pebbles and microaggregated organic loam with abundant charcoal, exceptionally well preserved uncharred plant remains and phytoliths (Supplementary Figure 4). Many of the plant remains are probably palm fronds (identified by the presence of articulated phytoliths). Larger calcitic particles within the ash deposits may be burned snail shells. Angular microflakes or clear quartz probably originated as knapping residue. Alongside bioturbation by mesofauna, which accounts for the crumb microstructure of loamy deposits, the most striking postdepositional changes of these early occupation deposits are diagenetic: pervasive phosphatisation of ash, dissolution of bone and ash, and growth of xenotropic gypsum nodules that disrupt the primary lamination of ash deposits. These diagenetic products, similar to those reported from guano-rich deposits of other tropical^{1,2} and temperate^{3,4} caves, suggest that bat guano was deposited in Fa-Hien Lena, perhaps between episodes of human occupation.

Stratigraphically higher Phase D deposits contain layers of structureless, pebbly ash with angular gneiss clasts and numerous burning residues (wood charcoal, burned bone, snail shell, abundant phytoliths and burned sediment intraclasts, interpreted as rip up clasts) floating in a matrix of rhombic calcite crystals (derived from wood ash). These are interpreted as midden deposits, resulting from the dumping and/or colluvial reworking of human occupation debris – predominantly hearth and cooking residues – into the back of the cave. Upper Phase D deposits, immediately under the large gneiss slabs (correlative with context 157(?) in the 2010 excavation: Supplementary Figure 2) are matrix-supported organic breccia with abundant burned and unburned biogenic residues (including well preserved fragments of *Canarium* sp. shells) in a

matrix of silty clay and (local) accumulations of calcite rhombs (reworked wood ash). Imbrication of gneiss pebbles/granules and other platy particles suggests deposition from flow – probably surface wash – directed towards the cave interior. These deposits are also interpreted as colluvia originating in middens or other habitation floor deposits.

Phase D sediments, therefore, record intermittent/episodic human occupation, from around 48,000 – 34,000 cal. BP (MIS 3) and colluvial inwash, during a period of structural instability of cave walls and ceiling (which accounted for the roof fall blocks embedded within the fine-grained facies of this phase). The latest of these roof fall episodes appears to have contributed to the exceptional preservation of these deposits by sealing large parts of Phase D from later disturbance. Human-mediated deposits evidence hearth building and maintenance, cooking, consumption and discard of food remains (which included *Canarium* sp. and other, as yet unidentified plant remains), and, possibly, the use of palm fronds for the construction of artefacts (e.g., mats, sleeping platforms, baskets and similar containers, as inferred from other Pleistocene sites in Sri Lanka: e.g., Batadomba-lena³). The depositional and diagenetic history these sediments will be reported elsewhere.

Phase C: Terminal Pleistocene Occupation

Phase C sediments are a very heterogeneous mixture of dark colored (dark gray to brown), organics-rich sandy silty loams, sandy loams and matrix-supported breccia with abundant charcoal and ash. Ash and charcoal are mixed with detrital sediments and also present as distinct laminae or lenses. Phase C deposits are structured as sharp-based layers inclined towards the cave wall, or as fills of 10s-of-cm-sized pits. With the exception of charcoal and ash laminae, bedding is absent; clast-rich units are often structureless, with gneiss clasts positioned at high angle. Despite its relatively narrow temporal range (13,000-12,000 cal. BP), Phase C contains the densest concentration of artifacts and human occupation debris in the entire Fa-Hien stratigraphy.

Micromorphological analysis of one sample from basal Phase C deposits (near, or perhaps across the Phase D/C boundary: Supplementary Figure 1) shows a very sharp based accumulation of closely packed wood charcoal and other charred biogenic particles (other plant remains, bone, snail shell) in a matrix of fine grained charred organic debris. Elongate particles are imbricated and register parallel bedding. This deposit may have resulted from relatively high-energy floor wash (e.g. a coarse lag formed in a floor depression) or from dumping or raked hearth residues. Calcitic ash, conspicuously absent from these burning residues, may have dissolved postdepositionally.

Truncation of stratigraphic boundaries, juxtaposed cut-and-fill features, absence of intrastratal structure and the overall mixed aspect of its deposits suggest that Phase C resulted from a succession of erosion, colluviation and, perhaps, dumping episodes. It is difficult to work out the relative chronology of these episodes based on current evidence. Floor hollows were excavated in floor wash colluvia (perhaps also including mass flow deposits) rich in reworked human occupation debris, and other occupation debris-rich deposits dumped or deposited *in situ* at the rear of the cave.

Colluviation and dumping of excavated debris could have resulted in mixing of charcoal and other datable sediment components of different ages; yet such mixing is not apparent in the

current set of dates. The clustering of radiocarbon dates around 13,000 to 12,000 cal. BP. may indicate rapid deposition.

Phase B: Early Holocene Occupation

Phase B is made up of two distinct lithostratigraphic units separated from the Terminal Pleistocene deposits by a sharp boundary that truncates underlying strata. The first unit consists of a series of subhorizontal layers of light brown sandy silts, matrix-supported collapse breccia and ash accumulations, with a moderate amount of artifacts and habitation debris, interpreted as undisturbed occupation deposits and floor wash colluvia (in contrast to the dumped and reworked deposits of Phase C). The second unit includes a large (diameter: 85 cm, depth: 80 cm), multi-stage pit and its fill. The pit fill, dated to ca. 8000-7700 cal. BP., consists of multiple layers of sandy silt and steeply-dipping accumulations of ash with abundant charcoal, much of which is charred *Canarium* sp. endocarps. Fire-reddening of the immediate substratum of some ash deposits suggests that burning may have taken place *in situ*; structureless mixtures of ash and charcoal may have resulted from deliberate ash dumping. Other fill units may have been deposited through floor wash and related colluvial processes.

Phase A: Mid-Holocene Occupation

Like Phase B, Phase A also comprises two distinct stratigraphic units. The first unit is composed of brown sandy loams and lenses of *Canarium* endocarp charcoal deposited directly above the pit. These deposits appear to have resulted from the building of hearths *in situ* (the thick accumulation of charred *Canarium* endocarp may represent several burning episodes on the same spot) followed by colluvial deposition on the cave floor. This unit is dated to ca. 5900 cal. BP. Above these deposits come ca. 25-35 cm of sharp-based, brown sandy and silty clays with little internal structure. These deposits are interpreted as dumps, derived from prehistoric habitation contexts. Dates of ca. 4700-4500 cal. BP. have been published⁴. Overlying the Mid-Holocene deposits is a thick brown sandy silt layer with high density of spalls followed by subhorizontal layers of sandy silty loams immediately under the present cave floor. These deposits resulted from extensive mining of the cave floor for fertilizer in the recent period, and even more recent colluvial deposition on the cave floor.

Supplementary Table 1. Radiocarbon dates from the 1986 excavations⁵.

Sample[*]	Context	Lab. Code	Measured
B-N5-2	2	Beta-33297	4,750 ± 60
B-M6-2	3	Beta-33293	6,850 ± 80
B-N6-2a	3a	Beta-33298	7,100 ± 60
B-M7-3	4	Beta-33295	24,470 ± 290
B-N7-3	4	Beta-33299	30,060 ± 290
B-M7-5	4a	Beta-33296	32,060 ± 630
B-M6-6	5	Beta-33294	33,070 ± 630

Supplementary Table 2. Radiocarbon dates from the 2010 excavations.

Sample[†]	Context	Measured	Conventional
BYP2010/CX NE/N-4, O-4, 107	107	3910 ± 30	3870 ± 30
BYP 2010 CX NE/O-6, 0-6, 116 middle	116	4,870 ± 40	4,800 ± 40
BYP2010/CX NE/N-4, O-4, 109	109	10,220 ± 40	10,150 ± 40
BYP 2010 CX NE/O-4, P-4, 108	108	33,260 ± 240	33,220 ± 240
BYP2010/CX NE/N-4, O-4, 110	110	36,950 ± 300	36,910 ± 300
BYP 2010 NE/O-4, 118	118	31,770 ± 190	31,750 ± 190
BYP 2010 CX NE/O-4, P-4, 119	119	10,300 ± 40	10,250 ± 40
BYP 2010 CX NE/ O-4, 126F	126	37,260 ± 310	37,230 ± 310

Supplementary Table 3. Radiocarbon dates from the 2012 excavation.

Sample[†]	Context	Lab. Code	Measured	Conventional
135	31/32/135	Beta-354907	4,860 ± 30	4,820 ± 30
152	51/152	Beta-354916	7,030 ± 40	6,990 ± 40
152	51/152	Beta-355793	7,300 ± 40	7,240 ± 40
153	52/153	Beta-354917	7,040 ± 40	6,900 ± 40
136	136	Beta-354908	7,010 ± 30	6,970 ± 30
138	138	Beta-354909	7,750 ± 40	7,720 ± 40
237	237	Beta-354921	10,460 ± 40	10,390 ± 40
139	139/140	Beta-354910	10,390 ± 40	10,350 ± 40
141	141	Beta-354911	10,440 ± 40	10,340 ± 40
142	142	Beta-354912	10,500 ± 40	10,430 ± 40
174	174/246	Beta-354919	10,490 ± 40	10,440± 40
144	144/161/164	Beta-354913	10,330 ± 40	10,290 ± 40
145	145	Beta-354914	32,920 ± 240	32,890 ± 240
175	175	Beta-354920	34,610 ± 320	34,600 ± 320
159	159	Beta-354918	43,030 ± 720	43,000 ± 720

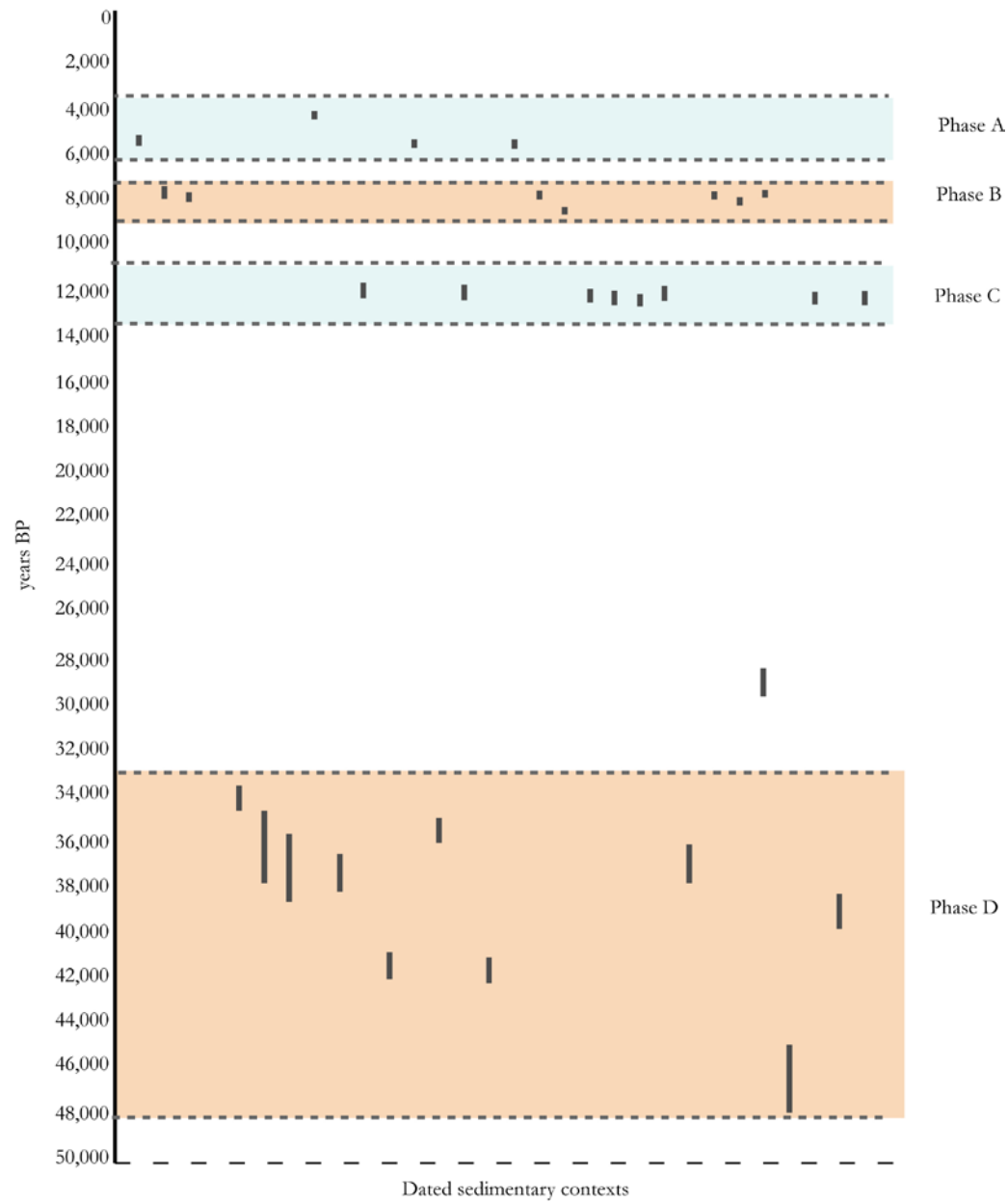
Supplementary Table 4. Calibrated radiocarbon dates for Fa Hien-lena.

Sample	Context	Calibrated (cal. years BP)[‡]
BYP2010/CX NE/N-4, O-4, 107	107	4,422-4,248
B-N5-2	2	5,594-5,322
135	31/32/135	5,653-5,488
BYP 2010 CX NE/O-6, O-6, 116 middle	116	5,710-5,482
B-M6-2	3	7,916-7,570
136	136	7,935-7,762
152	51/152	7,954-7,763
153	52/153	7,955-7,791
B-N6-2a	3a	8,020-7,794
152	51/152	8,180-8,020
138	138	8,595-8,430
BYP2010/CX NE/N-4, O-4, 109	109	12,096-11,768
BYP 2010 CX NE/O-4, P-4, 119	119	12,380-11,844
144	144/161/164	12,386-11,910
139	139/140	12,419-12,062
141	141	12,530-12,120
237	237	12,549-12,131
174	174/246	12,575-12,150
142	142	12,590-12,236
B-M7-3	4	29,126-27,872
B-N7-3	4	34,656-33,686
BYP 2010 NE/O-4, 118	118	36,136-35,191
B-M7-5	4a	37,912-34,764
145	145	37,912-36,300
B-M6-6	5	38,826-35,828
BYP 2010 CX NE/O-4, P-4, 108	108	38,333-36,690
175	175	39,876-38,490
BYP2010/CX NE/N-4, O-4, 110	110	42,036-40,980
BYP 2010 CX NE/ O-4, 126F	126	42,228-41,258
159	159	48,046-45,028

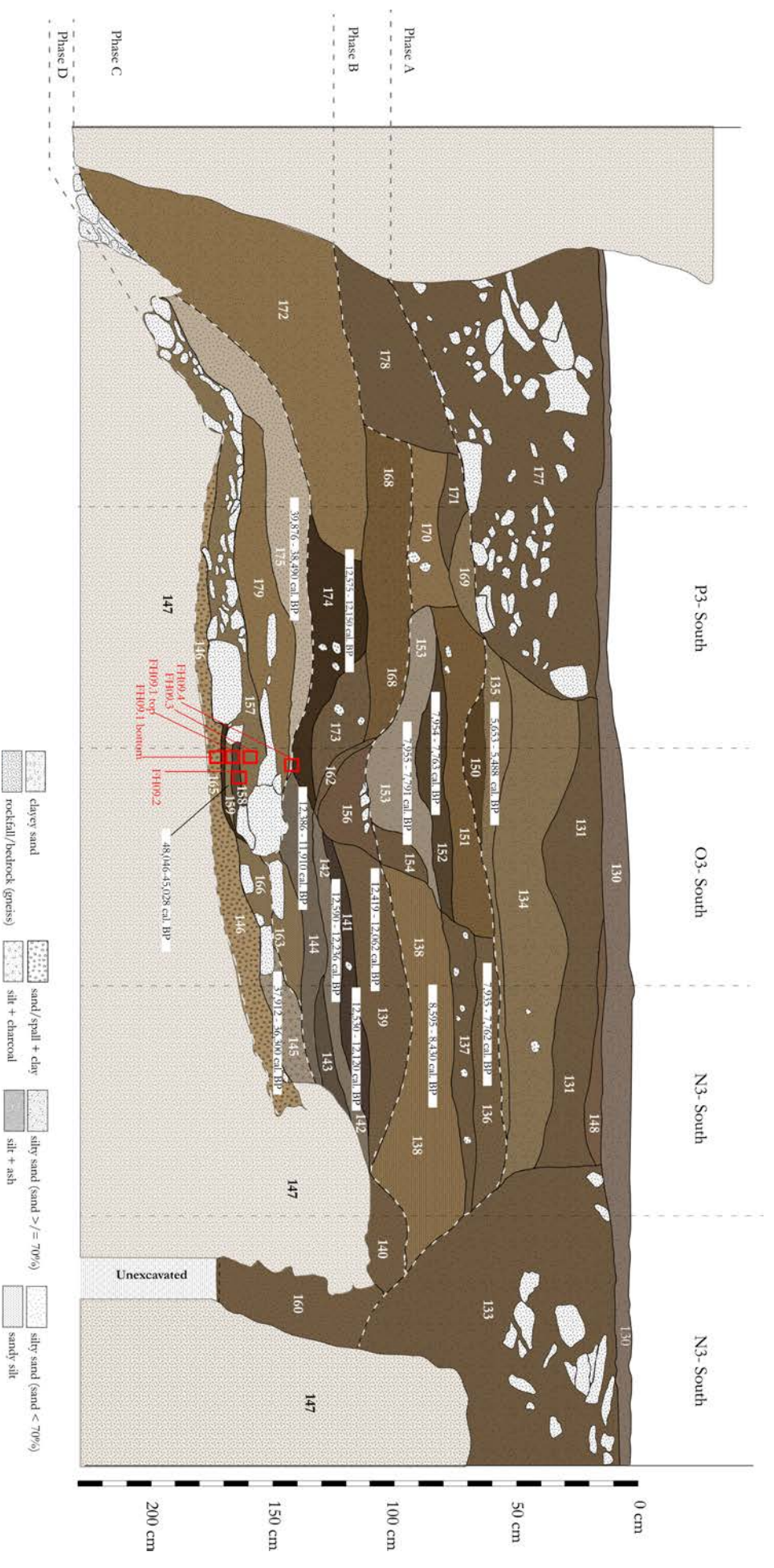
* Bulk radiocarbon measurement made on charcoal.

† AMS radiocarbon dates

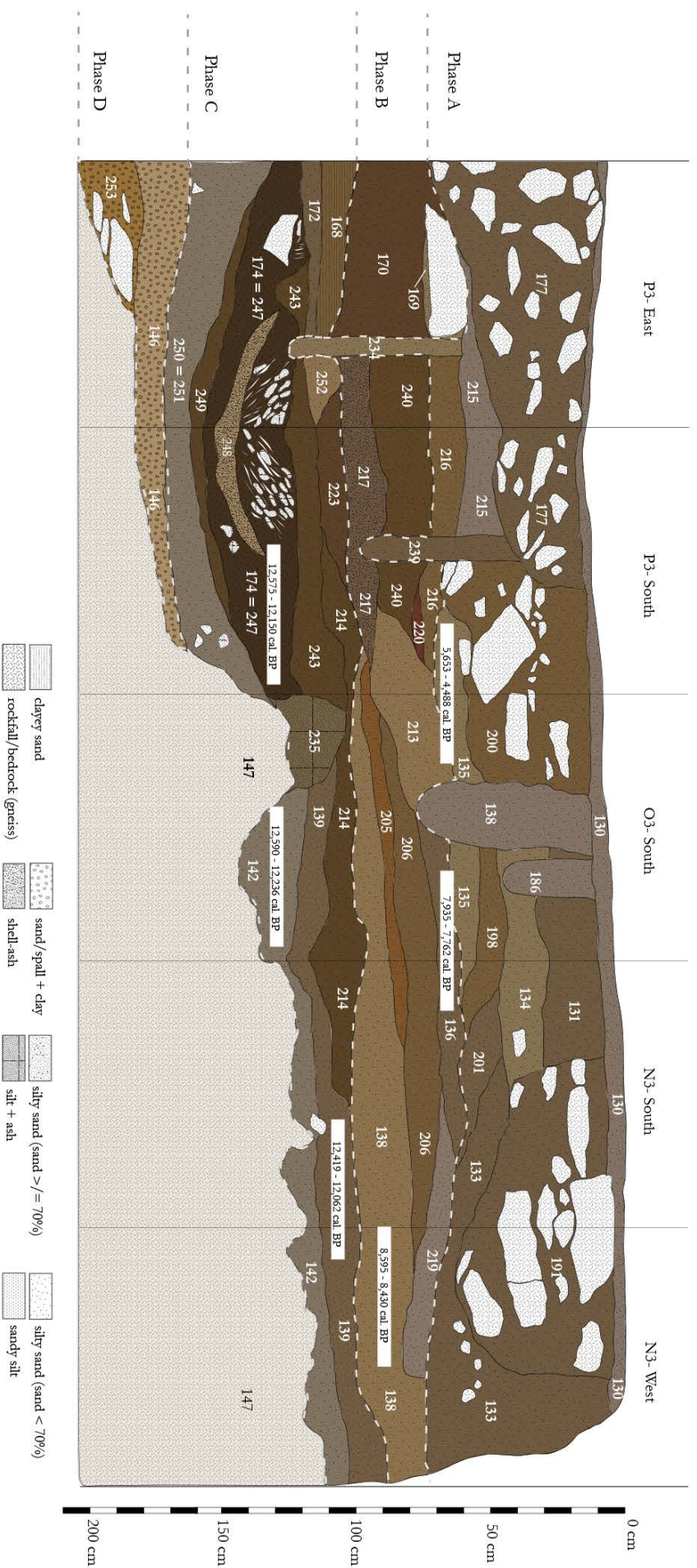
‡ All samples have been calibrated using the OxCal 4.3⁶ software and IntCal calibration curve⁷.



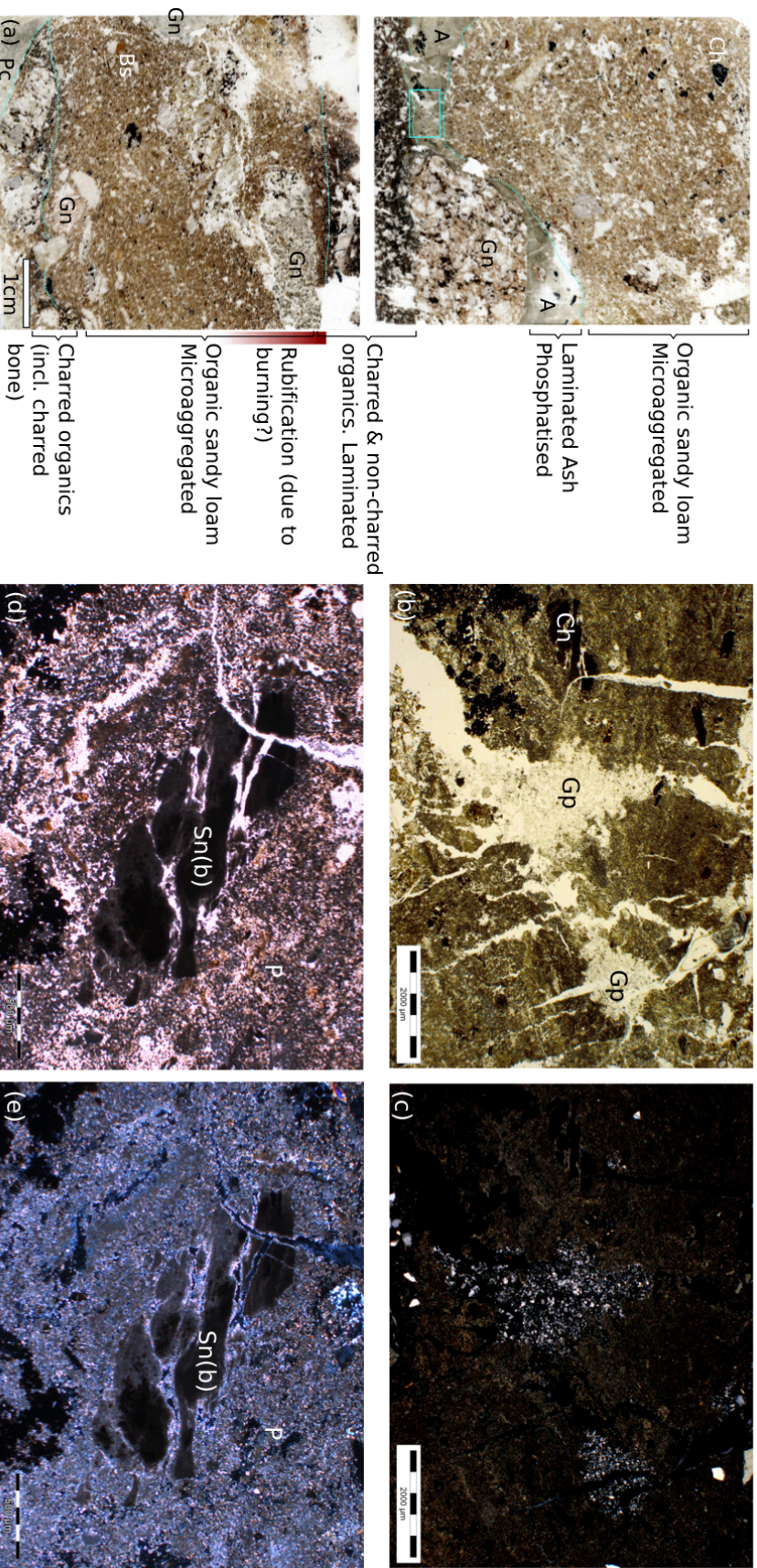
Supplementary Figure 1. Phases of human occupation in Fa-Hien Lena based on radiocarbon dates (cal. years BP) See Supplementary Table 4 for the list of dated sedimentary contexts.



Supplementary Figure 2. Stratigraphy of Fa-Hien Lena, (south wall end of the 2010 excavation, colors represent Munsell color values of sediments). Frames: correlative stratigraphic position of thin section micromorphology samples collected in the 2009 excavation.



Supplementary Figure 3. Stratigraphy of Fa-Hien Lena (south wall end of the 2012 excavation, colors represent Munsell color values of sediments).



Supplementary Figure 4. Micromorphology of Phase D sediments. a: Contiguous sections across basal Phase D deposits (scanned thin sections) reveal microstratified human occupation layers with evidence for *in situ* burning. Frame shows location of (b) and (c). A: ash; Bs: burned sediment (intraclast); Ch: charcoal; Gn: gneiss clast; Gp: P: amorphous phosphates. b and c: Microlaminated phosphatised ash and charred organics (Ch). Phosphatisation of the ash and growth of gypsum (?) nodules (Gp) were probably linked with the diagenesis of bat guano. d and e: Charred and heat-fissured calcitic particle (Sn(b)), probably snail shell, in a matrix of ash-derived calcite and amorphous phosphate (P). Some of the calcitic matrix is recrystallized. b, d: PPL; c, e: XPL.

Appendix 2. Further detail relating to analyses of faunal remains from Fa Hien Lena

A total of 14,485 bone fragments were analyzed from the approximately 150,000 specimens recovered during the 2010 and 2012 excavations of the cave. Of these, 16% were from the Late Pleistocene deposits, 45.7% from the Terminal Pleistocene (the most intense period of cave occupation), 31.8% from the Early Holocene, and 6.6% were from the Mid-Holocene layers. Supplementary Table 5 details the number of bone fragments studied per sedimentary context.

Bones are well preserved in all layers, with less than 1.4% of the specimens studied exhibiting moderate or heavy weathering (Supplementary Figure 6). Abraded bone fragments are also rare, with only 0.4% showing moderate to heavy abrasion. In Phase C, 2.1% exhibited evidence for hydrologic rounding, supporting the notion that the Late Pleistocene deposits consist mostly of redeposited habitation debris. In terms of bone fragment size, 83.4% of the specimens studied measured less than 30 mm, with an average bone fragment size of 22.35 mm (Supplementary Figure 7).

A total of 7622 specimens (52.6%) were identified to taxon (Supplementary Table 6). Small mammals dominate the assemblage, representing 95.5% of the total mammalian bone fragments studied and 95.2% of the mammalian specimens identified to taxon (Supplementary Table 7). In all phases of site occupation, small mammals account for more than 90% of the number of specimens. Large ungulates, including cervid, suids, and bovids are present all throughout the stratigraphy but in very small frequency (<4%). Fish, birds, and reptiles are present in slightly higher percentages. Non-mammalian fauna represent 13.5% and 5.9% of the specimens identified in Phase D and Phase C, respectively. Several reptile bone fragments, particularly varanids and *Python*, exhibit burning (58.2% NISP), suggesting that they were also utilized as a food source.

Supplementary Table 8 summarizes the vertebrate taxa recorded in Fa-Hien Lena. Cercopithecoid monkeys dominate the faunal assemblage of the site, representing 54.9% of the total number of specimens identified to taxon. A total of 589 cercopithecoid bone fragments from at least 27 individuals were recorded in the Late Pleistocene layers. These represent 48.7% of the specimens identified to taxon and 25.4% of the total number of faunal remains analyzed. Comparatively, a total of 2,138 cercopithecoid bone fragments from at least 62 individuals (Supplementary Table 9) were identified from the Terminal Pleistocene deposits of the cave, representing 57.6% of the specimens identified to taxon. Deliberate targeting of cercopithecoids by the people that occupied the cave continued until the Mid-Holocene, where cercopithecoid fragments represent 61.2% of the number of identified specimens. In addition to deliberate targeting of taxa, there also appears to be deliberate targeting of a certain age class. Mortality profile based on dental wear^{8,9} suggests that prime-age adults were targeted from the Late Pleistocene to the Mid-Holocene (Supplementary Figure 8-9).

Three cercopithecoid species are currently present in Sri Lanka: the cercopithecine *Macaca sinica* (toque macaque) and the colobine monkeys, *Trachypithecus vetulus* (purple-faced langur), and *Semnopithecus priam* (tufted gray langur). The three species occur sympatrically in Sri Lanka and all were identified in the faunal assemblage of Fa-Hien Lena. The cercopithecoid specimens in the assemblage were differentiated based on morphology of certain dental¹⁰⁻¹⁶ and skeletal elements¹⁷⁻¹⁹. Of the 4,188 cercopithecoid bone fragments recorded in the site, 318 specimens (7.6%) were identified to species, with *M. sinica* (49.4%) being more common than *T. vetulus*

(34.6%) and *S. priam* (16%). In the Late Pleistocene layers, a total of 43 *M. sinica* specimens from at least five individuals were identified. This is in contrast to the number of *T. vetulus* (NISP= 23, MNI=3) and *S. priam* (NISP= 10, MNI=2) recorded from the same layers. But because the majority of the recorded cercopithecoid specimens were long bone shaft fragments that cannot be assigned to species, all remains from a specific phase of site occupation were considered as comprising a single analytical assemblage.

In the Late Pleistocene layers, 10.9% of the identified remains are skull fragments (Supplementary Table 10), 1.9% are fragments of the mandible, 9.2% are isolated teeth (Supplementary Table 11), 5.3% are vertebrae (Supplementary Table 12), and 72.7% are appendicular skeletal elements (Supplementary Table 13). All skeletal elements, including carpal and tarsal bones, are present in the assemblage suggesting that complete carcasses were brought to the site (Supplementary Table 14). Vertebra fragments are slightly underrepresented due to preservation bias and the difficulty of assigning highly fragmented specimens to taxon. Supplementary Table 15-29 details the number of cercopithecoid dental and skeletal elements recorded in other phases of site occupation, and Supplementary Table 30-33 (see also Supplementary Figure 10) shows the MNE and MAU counts obtained for the cercopithecoid skeletal elements in the assemblages.

A total of 64 skull fragments were recorded in the Late Pleistocene layers of the cave (Supplementary Table 10). These represent a minimum of seven crania, as suggested by the presence of seven left zygomatic bone fragments. Parietal and frontal bones are the most common skull elements in the assemblage but they are very fragmented and cannot be used to estimate the MNI/MNE. The mandible fragments (NISP= 11) from the Late Pleistocene layers of the site also account for at least seven individuals. The relatively equal number of skull and mandible fragments in the Late Pleistocene layers indicates that entire skulls were retained in the site. This is in contrast to the discrepancy observed between the number of skull and mandible fragments from Terminal Pleistocene layers of the site (Supplementary Table 25). A total of 264 skull fragments from at least 11 individuals (overlapping maxillae and frontal bones) were recorded in Phase C. By contrast, the 60 mandible fragments identified in the same layers represent at least 28 individuals. The same difference is observed when the number of isolated maxillary (NISP= 83, MNI= 7) and mandibular (NISP= 126, MNI= 14) teeth are considered. The paucity of monkey skulls in the Terminal Pleistocene layers of Fa-Hien Lena parallels the observations made by other authors²⁰⁻²³ in their analyses of faunal assemblages from sites in Island Southeast Asia. Since no taphonomic process can account for the differential preservation of skulls and mandibles, they posit that monkey skulls could have been selectively retained, perhaps as trophies, by the people that settled the site.

The almost equal number of scapula (NISP= 15, MNI= 7) and pelvis (NISP= 17, MNI= 7) fragments in the Late Pleistocene layers of Fa-Hien Lena further supports the idea that entire monkey carcasses were being brought to the site. The same is true for the Terminal Pleistocene layers of the site which also yielded the same number of scapula and pelvis fragments (Supplementary Table 27).

Fragments of the appendicular skeleton, particularly of the long bones, were the most common specimens recorded in the site. In the Late Pleistocene layers, long bone fragments account for 36.7% of the cercopithecoid specimens identified (Supplementary Table 14). The femur is the most common long bone represented in the Late Pleistocene assemblage, with a total of 82

identified fragments representing at least 28 elements, followed by the fibula (MNE= 13) and the tibia (MNE=12). There is an overrepresentation of hind limb over forelimb elements (78.9% difference in the MNE) in Phase D (Supplementary Table 30). This is not the case in the Terminal Pleistocene layers where there is only a 16.8% difference between arm and leg elements. All long bone elements are well represented in the Terminal Pleistocene and Early Holocene layers of the site. By contrast, hind limb and forelimb elements are overrepresented in the Late Pleistocene and mid-Holocene layers, respectively (Supplementary Figure 11). These differences are interpreted as being linked to changes in preference for skeletal element as material for bone tool production by the people that used the cave through time. Hind limb elements appear to have been selectively retained as materials for tool manufacture during the early phase of site occupation. Almost all of the osseous tools recovered from the Late Pleistocene layers of the site were manufactured from cercopithecoid fibula and femur shaft fragments. By contrast, tools and artifacts made from both hind limb and forelimb elements were recorded in number in the Terminal Pleistocene and Early Holocene assemblages. During the mid-Holocene, there was a change in preference towards ulna shaft fragments as material for tool production, although tools from femur and fibula were also made.

Tool manufacture could also explain the high level of bone fragmentation observed in all phases of site occupation. Supplementary Table 34 details the degree of fragmentation of cercopithecoid long bone elements as measured by NISP:MNE ratio²⁴ and fragment circumference/length completeness (see also Supplementary Figure 12). Only two complete cercopithecoid skeletal elements were recorded in the assemblage studied, two fibulae from the Holocene layers. In the Late Pleistocene layers, 59.7% of the identified cercopithecoid long bone fragments have less than half the original circumference and 73.1% measured less than half of the original length (i.e., Supplementary Figure 12). Fragments with preserved epiphyses are also very rare (NISP= 4). The femur is the most fragmented element, with 86.6% of the specimens having less than half of the original circumference. This is not surprising considering that manufacture of osseous tools from femur fragments involved breaking the bone into manageable segments before grinding them into the desired shape. This mode of tool production continued up to the Early Holocene, where 65.8% of the recorded femur fragments have less than half of the original circumference owing to the degree of working. Bone tools manufactured from femur shafts are rare in the mid-Holocene layers despite femur specimens being better preserved in these layers (76.5% of the specimens have the complete circumference).

Long bones of other small mammals are less fragmented compared to those of cercopithecoids, particularly in the Late Pleistocene layers (Supplementary Figure 13). For instance, 64.3% of the sciurid long bone fragments recorded in Phase D have a complete circumference and 49.2% have preserved epiphyses. Mouse-deer and small carnivore long bones from the same layers are also well preserved. Again, these data support the idea that fragmentation of cercopithecoid long bones relate to their use as the main material for bone tool manufacture. All osseous artifacts recorded in the Late Pleistocene layers of the cave were manufactured from cercopithecoid long bone elements.

Butchery marks were recorded in nine specimens (0.39% of the total number of fragments) from the Late Pleistocene layers of the cave, mostly in small carnivore and squirrel bone fragments (Supplementary Table 35). Evidence for butchery was rare in cercopithecoid bone fragments from Phase D, with only one cutmarked specimen recorded (a femur shaft fragment). By contrast, all

the viverrid and otter remains recorded in Phase D had cutmarks. For example, an otter (*Lutra lutra*) proximal humerus shaft with cutmarks on the posterolateral surface (Supplementary Figure 4B) was recovered from context 253, the earliest deposit in the site. Two squirrel long bone fragments with cutmarks were also recorded from Phase D (i.e. tibia shaft in Supplementary Figure 4A). The frequency of bones with butchery marks is slightly higher in the Terminal Pleistocene layers (0.98% of the total number of fragments) of the site. Similar to Phase D, however, cercopithecoid bone elements with evidence for butchery were also rare in the Terminal Pleistocene layers. From the 55 bone fragments with butchery marks, only three were from cercopithecoids. This is despite the presence of complete epiphyses where cutmarks are usually observed^{22, 23, 25, 26}. Like in Phase D, most of the cutmarks were recorded in giant squirrel (N=20) and viverrid/mustelid (N=23) femur and humerus specimens.

The locations of the cutmarks on the sciurid and small carnivore long bones were also consistent. In the femur, all the cutmarks were observed on the lateral and medial shaft near the distal articular end. On the humerus, the cutmarks were concentrated on the lateral/medial supracondylar ridge and on the area just above the lateral/medial epicondyle. The prevalence of cutmarked distal humerus fragments (40% of specimens with cutmarks) suggests a systematic butchery process that involved the disarticulation of the ulna from the humerus. Little can be said about the cercopithecoid carcass processing sequence during the Late/Terminal Pleistocene phases of the site because of the low frequency of skeletal elements with traces of butchery. Severe fragmentation of skeletal elements in the Late Pleistocene layers, in addition to high frequency of burning (see below), obscures the evidence for butchery. But this is not the case in the Terminal Pleistocene layers where there is better skeletal element preservation.

As mentioned earlier, fragments of bone finished tools, blanks, and waste pieces, were recorded in all phases of occupation suggesting the use of the cave as a site for osseous tool manufacture. The bone tools recovered from the Late Pleistocene layers of Fa-Hien Lena were all manufactured from cercopithecoid long bones, except for a worked macaque canine recorded from context 253. A total of 36 specimens with surface modifications consistent with bone tool manufacture were recorded in the Late Pleistocene layers of the site (1.3% of the total number of specimens studied). These include ten fragments of finished tools (i.e., those retaining diagnostic morphology, including tips of bone points/spatulas). The rest are fragments which represent either waste pieces or tool blanks.

Burning and calcination were the most common modifications observed in bone fragments from the Fa-Hien Lena assemblage (Supplementary Table 35). Burning was recorded in skeletal elements of all the taxa identified, including fish and reptiles. Indeed, burning and calcination were the only modifications recorded in skeletal elements of non-mammalian taxa. The amount of burnt and calcined fish remains is high with 77.8% of the identified remains burnt/calcined. By comparison, 58.2% of snake and lizard remains exhibited burning. A significant proportion of sciurid remains also exhibited evidence for burning (31%). This is in comparison to the 16.1% recorded burnt cercopithecoid remains. The patterns of burning, including the presence of burning marks in the inner skull as well as completely burnt /calcined carpals and tarsals, suggest that burning occurred after skeletal disarticulation and deposition.

Burnt and calcined specimens were recorded in all phases of site occupation, although they appear to be more common in the Late Pleistocene layers in terms of relative proportion. A total of 273 burnt bone and tooth fragments were recorded in Phase D, representing 11.8% of

specimens recovered. In addition, 12.1% of the specimens from these layers were either partially (N=179) or completely (N=102) calcined. In context 253, the oldest layer in the site, 27.7% of the recorded bone fragments were burnt or calcined. By comparison, 12.8% of the specimens from the Terminal Pleistocene layers showed evidence for burning and 7.1% were calcined. The proportion of burnt fragments was slightly lower in the Early (9.6%) and Mid-Holocene layers (5.1%) of the site.

Next to cercopithecids, sciurids were the most common taxa identified in the faunal assemblage of Fa-Hien Lena. A total of 2026 sciurid remains were recorded in the site, representing 26.6% of the total number of identified specimens and 13.9% of the fragments analyzed. Sciurid remains represent 27.6% of the specimens identified from the Late Pleistocene Layers, 27.1% of the specimens from the Terminal Pleistocene layers, and 28.8% and 10.2% of those from the Early and Mid-Holocene assemblages respectively. At least three squirrel taxa were identified in the assemblage based on the morphology of teeth and certain post-cranial elements: the giant grizzled squirrel *Ratufa macroura* and the flying squirrels *Petinomys* and *Petaurista*. The palm squirrel *Funambulus* might also be present in the assemblage, as some diagnostic elements including maxillae and mandibles were identified in layers not included in the present study (i.e., non-dated sedimentary contexts). Specimens that cannot be securely assigned to genus were identified to the family level.

Although both taxa were recorded in all the phases of site occupation, it appears that the people that utilized the site targeted *Ratufa* as a prey more than the flying squirrels. For instance, a total of 121 (36.2%) grizzled giant squirrel remains from at least 16 individuals were identified from the Late Pleistocene layers compared to the 20 *Petinomys/Petaurista* skeletal and dental elements from at least three individuals recorded from the same layers. Similarly, 41.6% of the sciurid remains from the Terminal Pleistocene layers were assigned to *R. macroura* and 4.3% were identified as from flying squirrels. *Petaurista* and *Petinomys* are both nocturnal, arboreal species. On the other hand, the grizzled giant squirrel, like the cercopithecids identified in the assemblage, is a diurnal, arboreal species. Because *Ratufa* and the cercopithecids occur in the same forest environment, it is most likely that they were encountered together by the people that settled the site. All sciurid skeletal elements were represented in all phases of site occupation (Supplementary Table 36-39, Supplementary Figure 14) indicating that entire carcasses were brought to the site. A high proportion of sciurid remains from the Late and Terminal Pleistocene levels were burnt and calcined (30.2% and 27.9% respectively). For instance, Supplementary Figure 15 shows *R. macroura* calcanei in different stages of burning and calcination. The presence of cutmarks on long bone epiphyses indicates disarticulation and division of carcasses into smaller units during butchery. Implements made from squirrel skeletal elements were rare (N=4, modified femur) and were only recorded in the Early and Mid-Holocene levels.

Other small mammals recorded in the Fa-Hien Lena assemblage include six different small carnivore taxa from four different families. Vivverids, the most common small carnivore in the assemblage, were represented by two genera: the palm civet *Paradoxurus* and the Indian civet *Viverricula*. These taxa were recorded in all phases of site occupation but in much lower frequencies compared to sciurids and cercopithecids. Herpestids and mustelids were also recorded from the Late Pleistocene to the Early Holocene layers of the site. As pointed out before, numerous small mammal long bone fragments exhibited evidence for butchery, as well as burning and calcination, suggesting that they were probably consumed. However, their low

frequency suggests that they did not play a major role in the subsistence of the people that utilized the site.

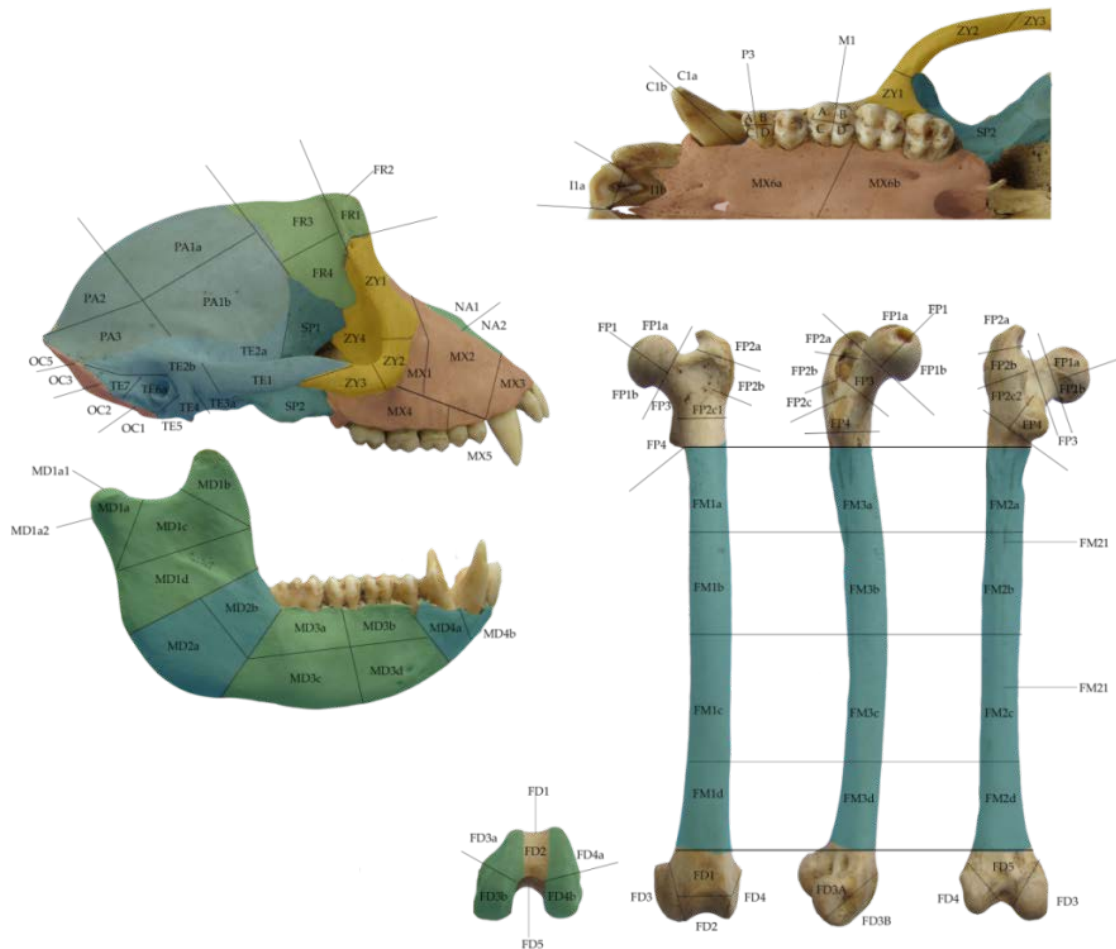
In addition to small carnivores, mouse deer (*Moschiola*) remains were also observed in all occupational phases of Fa-Hien Lena. The mouse deer skeletal elements did not yield any evidence for butchery, unlike those from the small carnivores. However, a significant proportion was burnt or calcined. For instance, 10 out of the 14 mouse deer specimens recorded from the Late Pleistocene layers were burnt. In the Terminal Pleistocene layers, 72% of the mouse deer remains exhibited evidence for burning or calcination. Like the small carnivores, mouse deer were probably utilized by the people that settled Fa-Hien Lena as a supplementary source of protein.

Large ungulates, including cervids, bovids, and suids, were recorded in all phases of site occupation, but in very low frequency. Elephants and rhinoceros were also identified, albeit only in the Terminal Pleistocene and Early Holocene layers. Interestingly, large ungulates were mostly represented in the assemblage by tooth or long bone fragments, suggesting that they were not butchered in the site. For instance, tooth fragments represent 21 out of the 31 suid specimens identified in the Terminal Pleistocene layers. Likewise, 56.6% of the cervid specimens from the same layers were molar/premolar fragments. At least two deer taxa were noted based on dental size. A complete lower third molar from the Terminal Pleistocene layers allowed the identification of the smaller taxon as the barking deer *Muntiacus muntjak*. The larger taxon cannot be assigned to genus because of the fragmentary nature of the specimens. Two large deer species are currently present in Sri Lanka: the spotted deer (*Axis* sp.) and the sambar deer (*Rusa unicolor*).

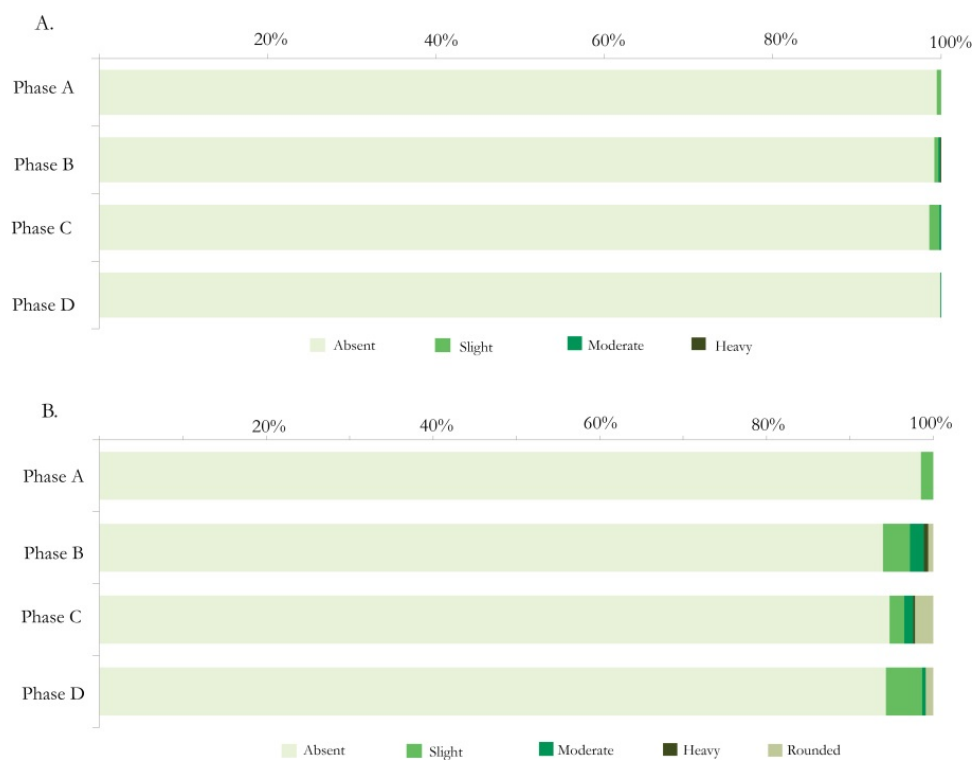
Elephants were also represented by tooth fragments, including a completely burnt neonate molar from the Terminal Pleistocene layers. The presence of a rhinoceros upper molar fragment in Phase B indicates the presence of this species as far south as Sri Lanka's Western Province during the early Holocene. In the Late Pleistocene layers, large ungulates were also represented mostly by tooth fragments. For instance, two burnt bovid molar fragments were identified from a sediment layer dated to 39,876-38,490 cal. BP. Long bone fragments, the majority of which were worked, constitute the rest of the ungulate remains recorded in the site. Worked deer metapodials and antler fragments (N= 16) were recorded in the Terminal Pleistocene and Early Holocene layers of the site. The low frequency of large ungulate remains in the faunal assemblage suggests that they did not play a significant role in the subsistence of the people that settled the site. Instead, large ungulate skeletal and dental elements were most likely imported to the site as finished tools or as materials for tool production as evidenced by the high proportion of worked fragments.

Reptiles and fish were also recorded in all phases of site occupation. The fish remains from Fa-Hien Lena are represented by two families, silurids (catfish) and cyprinids (carps), identified from cranial elements. Complete pharyngeal teeth allowed the identification of the cyprinid in the assemblage as representing the genus *Tor* (mahseer). Nonetheless, 71.5% of the fish remains recorded in the site are spine and vertebra fragments that cannot be identified to taxon. Butchery marks are usually rare in fish bones from archaeological sites^{27, 28}, and the fish remains from Fa-Hien Lena did not exhibit any evidence for butchery/processing. Anthropogenic modifications in fish bones from the site were restricted to burning. 77.8% of the total number of fish remains identified in the site were burnt or calcined. Interestingly, all fish bones from the Late

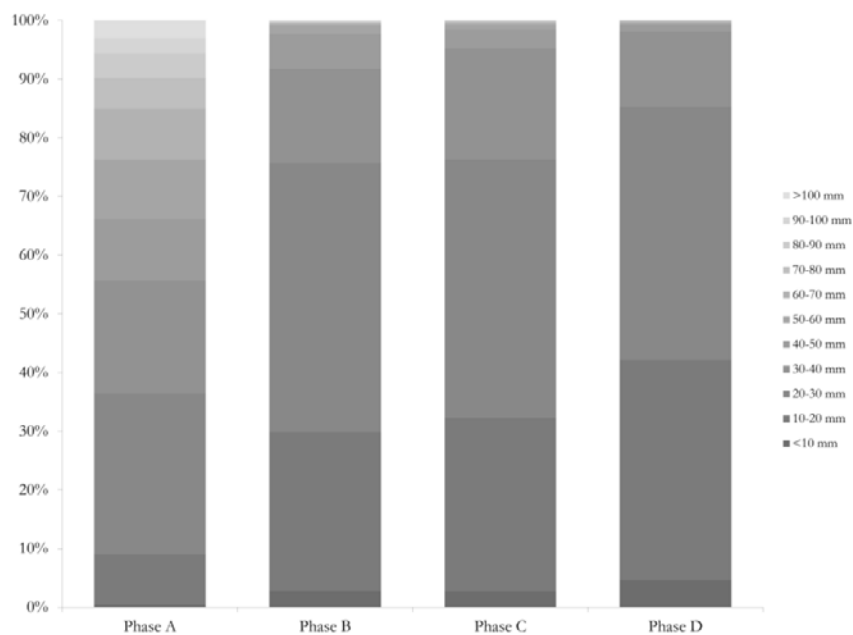
Pleistocene layers of the site exhibited evidence for burning (e.g., Supplementary Figure 16). Reptiles account for 4.4% of the total number of identified specimens from the Late Pleistocene layers and 5.9% of those from the Terminal Pleistocene. Reptiles are represented by pythons, colubrid snakes, water monitors, and dragon lizards as well as geckos and skinks. Crocodiles were recorded in the assemblage; but only in the Terminal Pleistocene layers. Butchery marks were not observed in any of the reptile skeletal elements examined and similar to fish bones, anthropic modifications were restricted to burning. 28.8% of the reptile remains identified in the site were burnt or calcined. In the Late Pleistocene layers, 74.1% of the monitor lizard remains and 85.7% of the snake specimens exhibited burning.



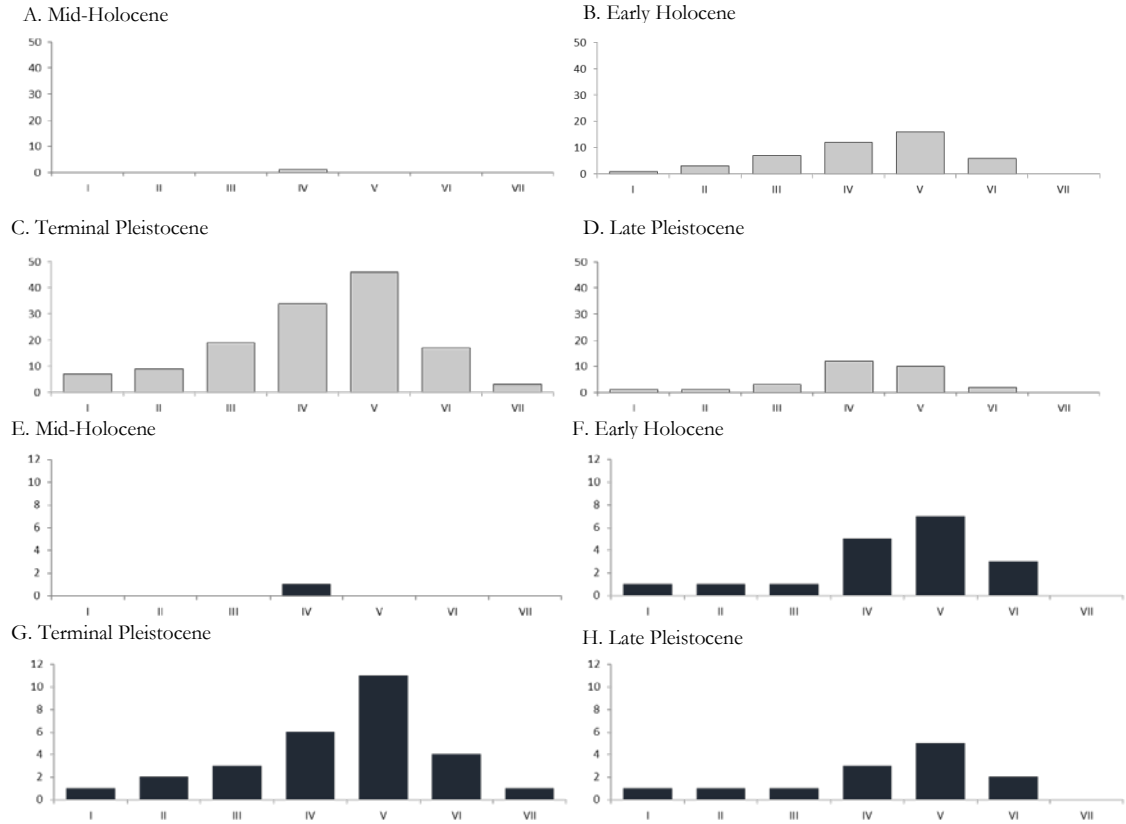
Supplementary Figure 5. Example of the system for recording bone fragments used in the current study.



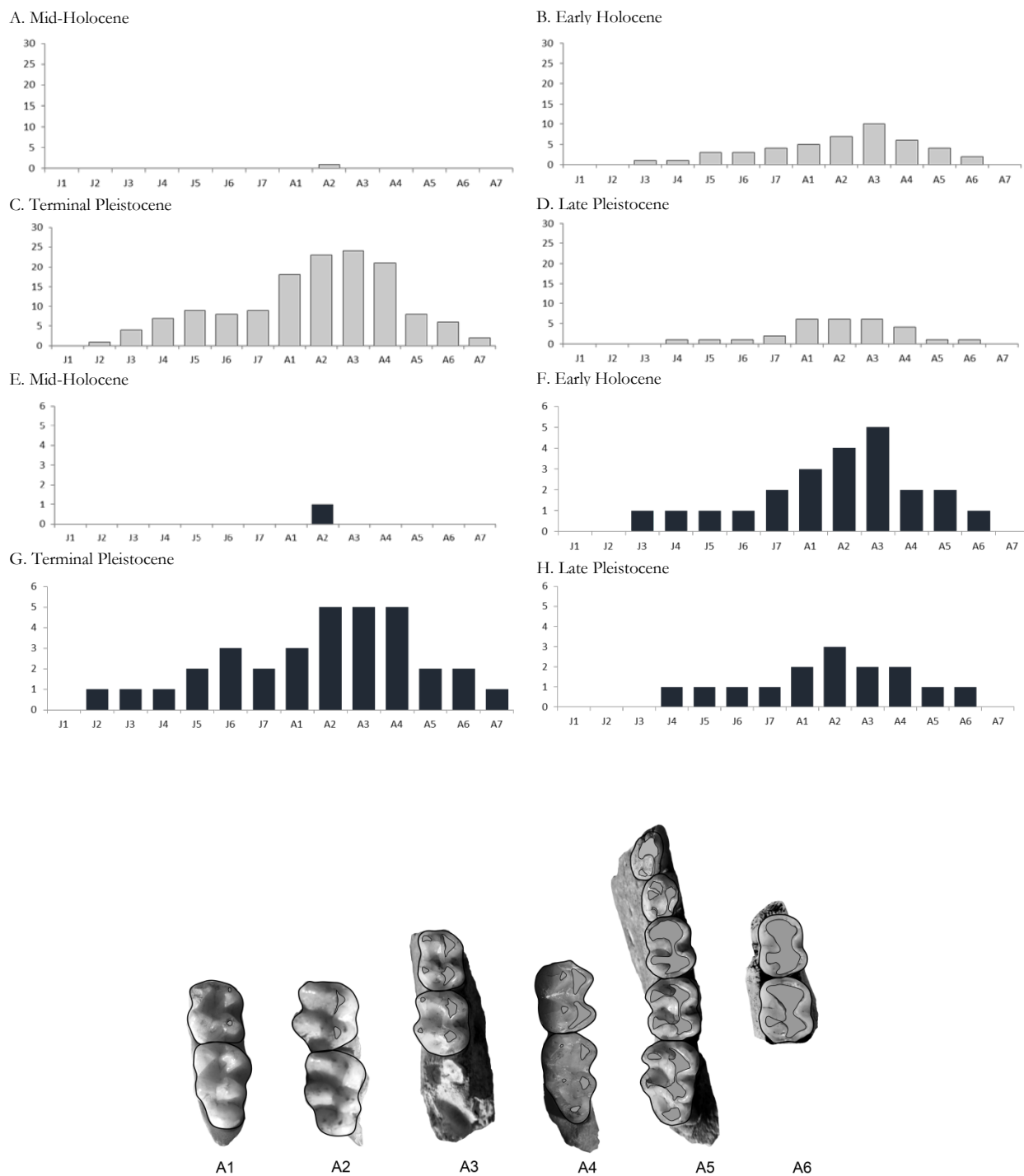
Supplementary Figure 6. Distribution of bone fragments based on abrasion (A) and weathering (B) in the different occupational phases Fa-Hien Lena.



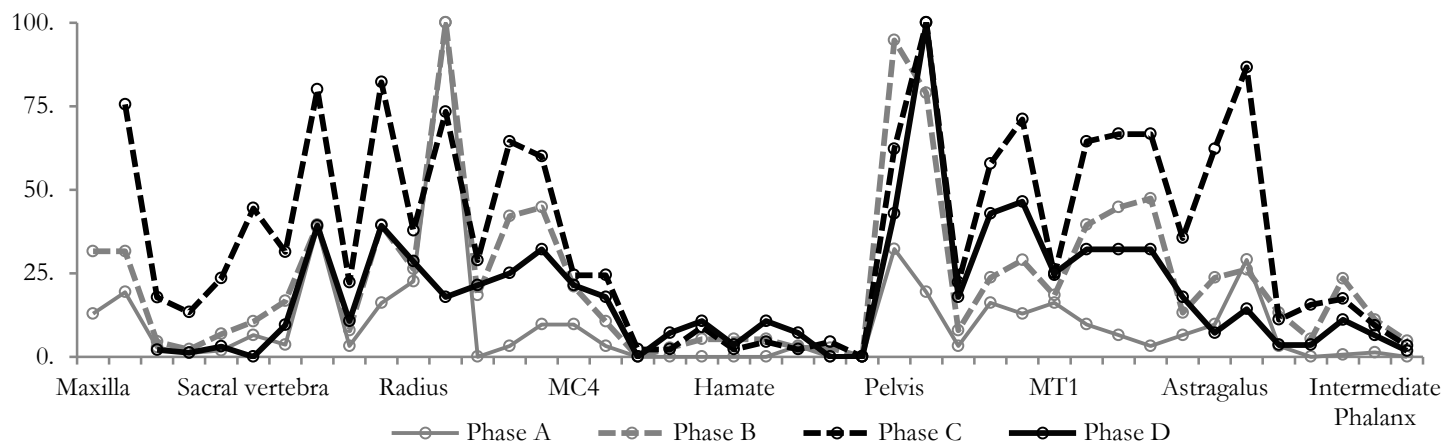
Supplementary Figure 7. Fragmentation (based on fragment length) of specimens recorded in the different occupational phases of Fa-Hien Lena.



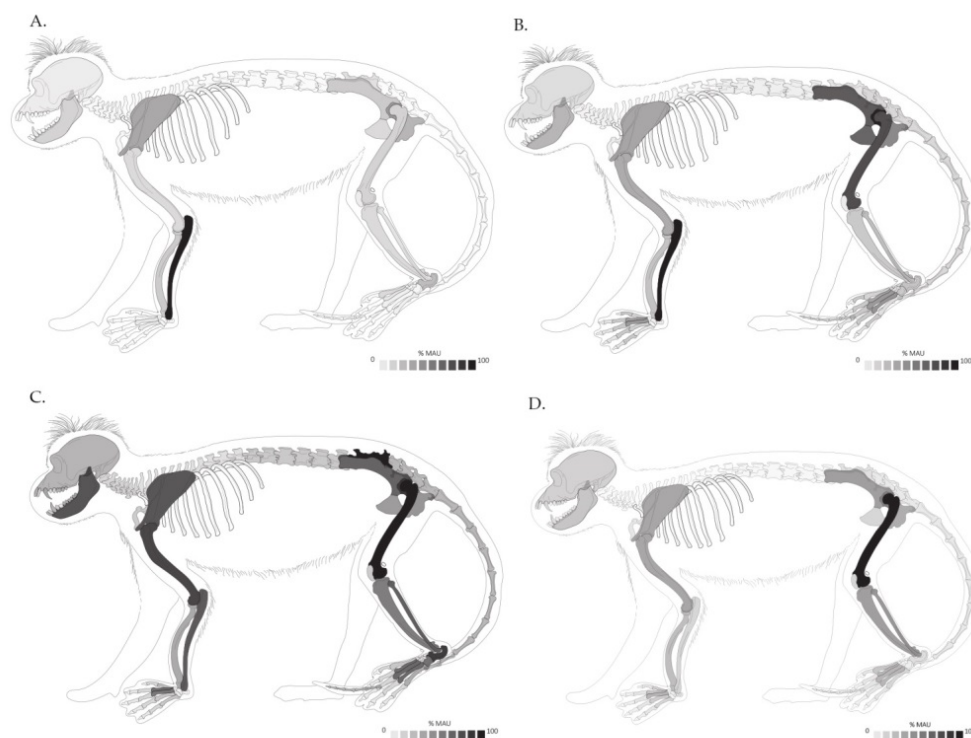
Supplementary Figure 8. Mortality profiles of cercopithecoid monkeys (following⁸) considering the NISP (A-D) and the MNI (E-H).



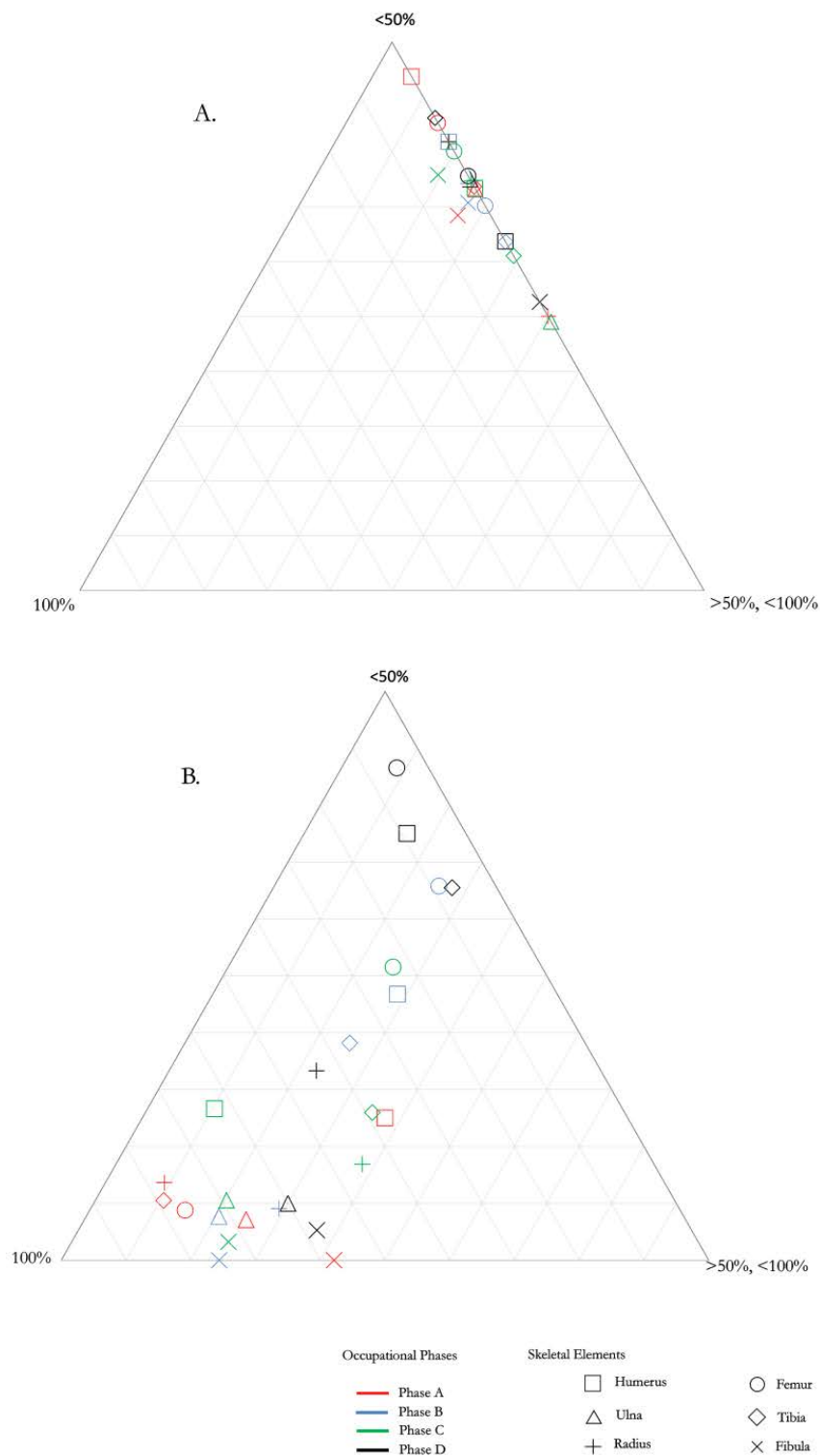
Supplementary Figure 9. Mortality profiles of cercopithecoid monkeys (following⁹) considering the NISP (A-D) and the MNI (E-H).



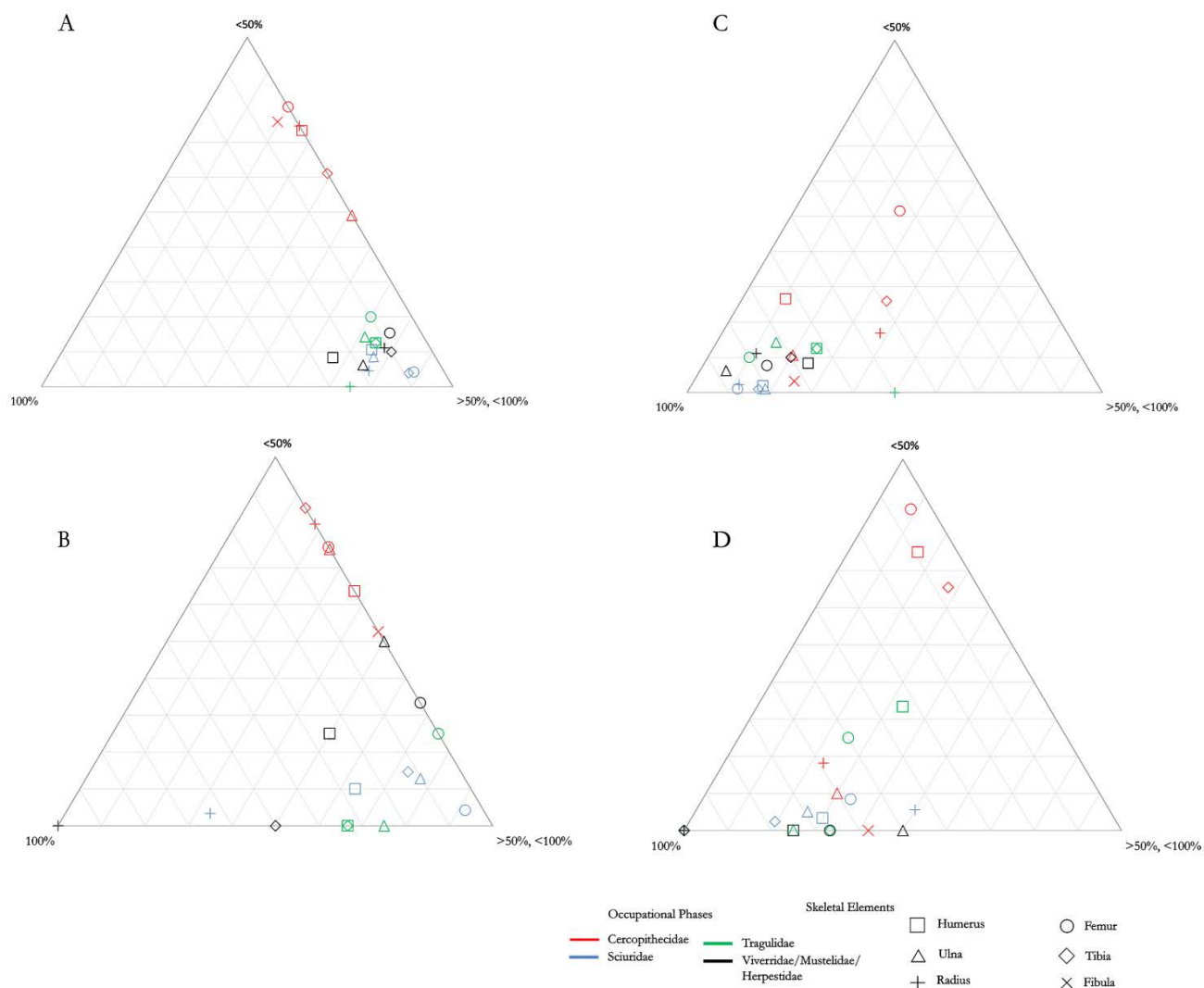
Supplementary Figure 10. Body part representation (% MAU) of cercopithecids in the different phases of occupation of Fa-Hien Lena.



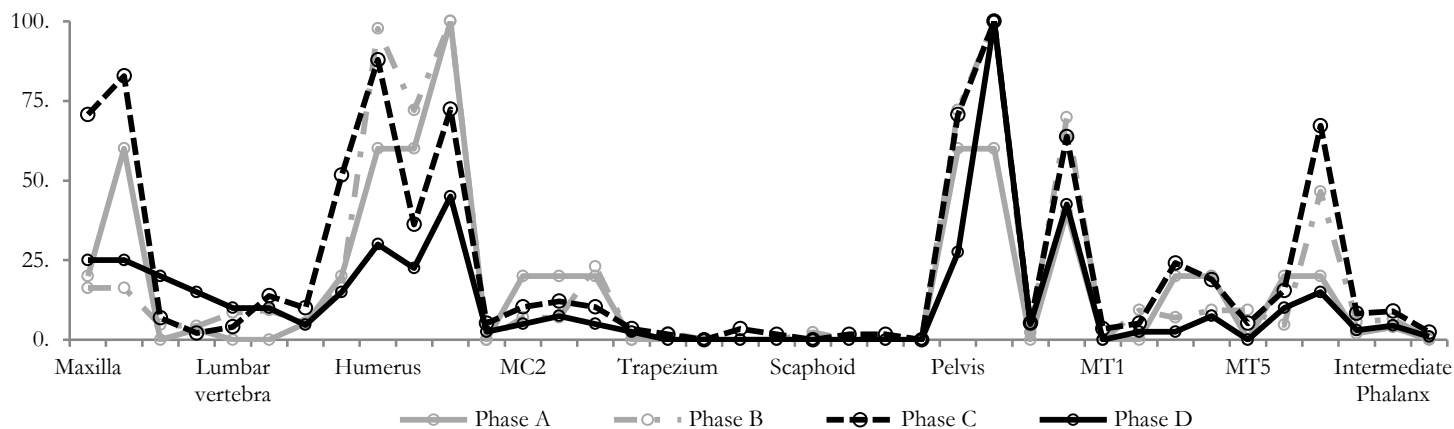
Supplementary Figure 11. Cercopithecid skeletal element representation in Fa-Hien Lena considering the % Minimum Number of Animal Unit (%MAU). A- Phase A, B- Phase B , C- Phase C, D- Phase D.



Supplementary Figure 12. Ternary scatter plot illustrating cercopithecoid long-bone length (A) and circumferential completeness (B).



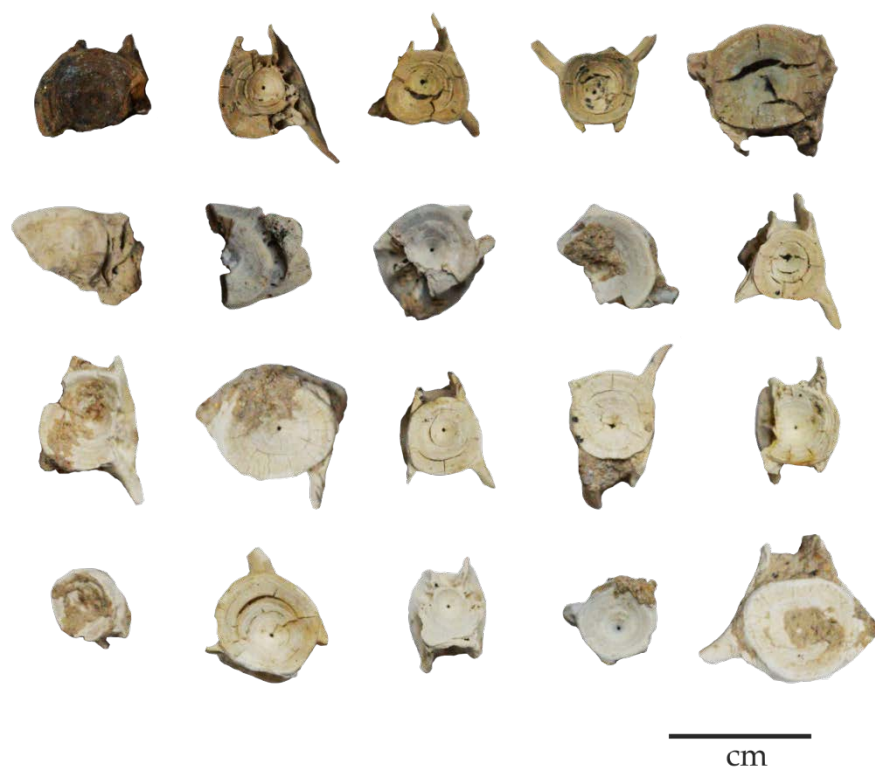
Supplementary Figure 13. Ternary scatter plot illustrating small mammal long-bone fragmentation (**A**- Terminal Pleistocene, length completeness; **B**- Late Pleistocene, length completeness; **C**- Terminal Pleistocene, circumferential completeness; **D**- Late Pleistocene, circumferential completeness).



Supplementary Figure 14. Body part representation (% MAU) of sciurids in the different phases of occupation of Fa-Hien Lena.



Supplementary Figure 15. *Ratufa macroura* calcanei in different stages of burning/calcination from the Late Pleistocene deposits of Fa-Hien Lena (measurement bar= 1 cm).



Supplementary Figure 16. Fish vertebrae in different stages of burning/calcination from the Late Pleistocene deposits of Fa-Hien Lena.

Supplementary Table 5. Number of bone fragments from different sedimentary contexts that were included in the current study

Phase	Context	Date	Number of fragments analyzed	Total number of fragments
A	216		661	956
	131		114	
	31/32/135	5653-5488 cal. BP.	181	
B	7/151	7955-7791 cal. BP.	62	4595
	52/153		451	
	170		188	
	116/128	7935-7762 cal. BP.	2281	
	180		380	
	136		535	
	38/206	8595-8430 cal. BP.	193	
	138		210	
	98		35	
	107		260	
C	168		87	6615
	237		93	
	139/140	12,419-12,062 cal. BP.	576	
	141	12,530-12,120 cal. BP.	94	
	173		605	
	142	12,590-12,236 cal. BP.	207	
	248		2354	
	174/247	12,575-12,150 cal. BP.	2294	
	144/161/164	12,386-11,910 cal. BP.	245	
	163/235	13,085 +/- 75	60	
D	108		318	2319
	110		414	
	118		238	
	145	37,912-36,300 cal. BP.	36	
	179		132	
	175	39,876-38,490 cal. BP.	288	
	157		55	
	158	40,250 +/- 650	64	
	159	48,046-45,028 cal. BP.	31	
	165	42,800 +/- 900	38	
	253		705	
Total				14,485

Supplementary Table 6. Number of identified specimens (NISP) in the different occupational phases of Fa-Hien Lena.

	Phase A	Phase B	Phase C	Phase D
Unidentified Bone Fragments	467	2384	2903	1109
NISP	489	2211	3712	1210
Percentage NISP	51.2	48.11	56.1	52.2

Supplementary Table 7. Distribution of mammalian taxa grouped by body size in the different occupational phases of Fa-Hien Lena.

Unidentified Mammalian Bone Fragments	Phase A	Phase B	Phase C	Phase D
Micromammals- 100g to 1 kg	11	18	4	16
Small mammals- 1 kg to 25 kg	447	2325	2772	1059
Large mammals class 1- 25 kg to 200 kg	8	40	112	22
Large mammals class 2- 200 kg to 1000 kg	1	1	12	10
Large mammals class 3: >1000 kg	0	0	3	2
Total Unidentified Bone Fragments	467	2384	2903	1109
Identified Mammalian Bone Fragments	Phase A	Phase B	Phase C	Phase D
Micromammals- 100g to 1 kg	8 (2.12%)	65 (3.28%)	74 (2.12%)	99 (9.46%)
Small mammals- 1 kg to 25 kg	360 (95.24%)	1884 (95.10%)	3275 (93.84%)	936 (89.40%)
Large mammals class 1- 25 kg to 200 kg	8 (2.12%)	29 (1.46%)	125 (3.58%)	10 (0.96%)
Large mammals class 2- 200 kg to 1000 kg	2 (0.53%)	1 (0.05%)	15 (0.43%)	2 (0.19%)
Large mammals class 3: >1000 kg	0	2 (0.10%)	1 (0.03%)	0
Total Mammals (NISP)	378	1981	3490	1047
Total Mammalian Bone Fragments	Phase A	Phase B	Phase C	Phase D
Micromammals- 100g to 1 kg	19 (2.25%)	83 (1.9%)	78 (1.22%)	115 (5.33%)
Small mammals- 1 kg to 25 kg	807 (95.5%)	4209 (96.43%)	6047 (94.59%)	1995 (92.53%)
Large mammals class 1- 25 kg to 200 kg	16 (1.89%)	69 (1.58%)	237 (3.71%)	32 (1.48%)
Large mammals class 2- 200 kg to 1000 kg	3 (0.36%)	2 (0.05%)	27 (0.42%)	12 (0.56%)
Large mammals class 3: >1000 kg	0	2 (0.05%)	4 (0.06%)	2 (0.09%)
Total	845	4365	6393	2156

Supplementary Table 8. Number of identified specimens of the different vertebrate taxa identified in Fa-Hien Lena.

Class	Order	Family	Taxon	Common Name	Phase A		Phase B		Phase C		Phase D	
					NISP	% NISP	NISP	% NISP	NISP	% NISP	NISP	% NISP
Actinopterygii	Cypriniformes	Cyprinidae	<i>Tor</i> sp.	Mahseer	4	0.82	39	1.76	17	0.46	43	3.55
	Siluriformes	Siluridae		Catfish	-	-	13	0.59	10	0.27	5	0.41
					-	-	5	0.23	6	0.16	2	0.17
Amphibia	Anura				3	0.61	-	-	3	0.08	42	3.47
Aves	Apodiformes	Apodidae		Swift	1	0.2	5	0.23	7	0.19	-	-
	Passeriformes				1	0.2	1	0.05	2	0.05	-	-
					-	-	-	-	-	-	-	-
		Hirundinidae		Swallow	-	-	1	0.05	-	-	-	-
		Corvidae		Crow/Magpie	-	-	2	0.09	2	0.05	-	-
		Sturnidae		Starling	-	-	1	0.05	-	-	-	-
	Galliformes	Phasianidae	<i>Gallus</i> sp.	Junglefowl	2	0.41	4	0.18	12	0.32	-	-
	Strigiformes	Strigidae		Owl	1	0.2	1	0.05	1	0.03	-	-
Reptilia	Crocodylia	Crocodylidae	<i>Crocodylus</i> sp.	Crocodile	-	-	-	-	4	0.11	-	-
	Testudines	Bataguridae		Terrapin	-	-	-	-	-	-	1	0.08
	Squamata	Varanidae	<i>Varanus</i> sp.	Monitor lizard	18	3.68	47	2.13	73	1.97	27	2.23
		Agamidae		Agamid lizards	6	1.23	10	0.45	6	0.16	6	0.5
		Geckonidae/Scinicidae		Gecko/Skink	6	1.23	1	0.05	-		2	0.17
		Pythonidae	<i>Python</i> cf. <i>molurus</i>	Indian Python	21	4.29	41	1.85	43	1.16	11	0.91
		Colubridae/Viperidae		Colubrid/Viper	48	9.82	59	2.6	36	0.97	24	1.98

Supplementary Table 8. continued

Class	Order	Family	Taxon	Common Name	Phase A		Phase B		Phase C		Phase D	
					NISP	% NISP	NISP	% NISP	NISP	% NISP	NISP	% NISP
Mammalia	Primates	Cercopithecidae			265	54.2	1071	48.43	2021	54.45	513	44.87
			<i>Macaca sinica</i>	Toque macaque	18	3.68	41	1.86	55	1.48	43	1.9
			<i>Trachypithecus vetulus</i>	Purple-faced langur	11	2.25	35	1.58	41	1.11	23	1.07
			<i>Semnopithecus priam</i>	Tufted gray langur	5	1.02	15	0.68	21	0.57	10	0.83
			<i>Loris</i>	Loris	-	-	-	-	3	0.08	-	-
	Rodentia	Hystriidae	<i>Hystrix cf. indica</i>	Indian porcupine	2	0.41	8	0.36	23	0.62	6	0.5
			Sciuridae	<i>Ratufa macroura</i>	21	4.29	332	15.02	545	14.68	193	15.94
					24	4.91	269	12.17	418	11.26	121	10
		Muridae	<i>Petionomys/Petaurista</i>	Grizzled giant squirrel Flying squirrel	5	1.02	35	1.58	43	1.16	20	1.64
					1	0.2	16	0.72	17	0.46	59	4.88
	Lagomorpha	Leporidae	<i>Lepus cf. nigricollis</i>	Indian hare	-	-	4	0.18	10	0.27	-	-
	Soricomorpha	Soricidae		Shrew	-	-	1	0.05	2	0.05	1	0.08
	Chiroptera				2	0.41	10	0.45	5	0.13	12	0.99
					-	-	-	-	2	0.05	2	0.17
					-	-	1	0.05	3	0.08	1	0.08
					-	-	2	0.09	2	0.05	3	0.25
					-	-	-	-	-	-	1	0.08
			<i>Pteropus</i> sp.	Short-nosed fruit bat Flying fox	-	-	11	0.49	3	0.08	2	0.17

Supplementary Table 8. continued

Class	Order	Family	Taxon	Common Name	Phase A		Phase B		Phase C		Phase D	
					NISP	% NISP	NISP	% NISP	NISP	% NISP	NISP	% NISP
Mammalia	Carnivora	Viverridae			4	0.82	32	1.45	46	1.24	5	0.41
			<i>Paradoxurus</i> sp.	Palm civet	3	0.61	5	0.23	18	0.48	3	0.25
			<i>Viverricula</i> sp.	Indian civet	1	0.2	2	0.09	2	0.05	-	-
			<i>Herpestes</i>	Mongoose	-	-	8	0.36	6	0.16	2	0.17
			<i>Lutra lutra</i>	Otter	-	-	3	0.14	17	0.46	1	0.08
			<i>Prionailurus</i> sp.	Spotted/Fishing cat	-	-	-	-	1	0.03	-	-
			<i>Felis</i> sp.	Jungle cat	-	-	-	-	2	0.05	-	-
			<i>Canis</i> cf. <i>aureus</i>	Golden jackal	-	-	4	0.18	11	0.3	-	-
		Artiodactyla	Tragulidae	<i>Moschiola</i> sp.	6	1.23	48	2.17	43	1.16	14	1.16
					1	0.2	4	0.18	31	0.84	2	0.17
					3	0.61	6	0.27	36	0.97	3	0.25
					2	0.41	7	0.32	19	0.51	3	0.25
		Bovidae	<i>Rusa unicorn</i> <i>/Axis</i> sp.	Deer	2	0.41	8	0.36	28	0.75	2	0.17
					2	0.41	8	0.36	28	0.75	2	0.17
					2	0.41	8	0.36	28	0.75	2	0.17
					2	0.41	8	0.36	28	0.75	2	0.17
		Perissodactyla	Rhinocerotidae	<i>Rhinoceros</i> sp.	2	0.41	1	0.05	15	0.4	2	0.17
					-	-	1	0.05	-	-	-	-
	Proboscidea	Elephantidae	<i>Elephas maximus</i>	Asian elephant	-	-	1	0.05	1	0.03	-	-
					-	-	1	0.05	1	0.03	-	-

Supplementary Table 9. Number of Identified Specimens (NISP) Minimum Number of Individuals (MNI) of cercopithecids and sciurids in the different occupational phases of Fa-Hien Lena.

Period	Context	Cercopithecids		Sciurids	
		NISP	MNI	NISP	MNI
A	216	230	14	16	2
	131	22	2	6	1
	31/32/135	47	3	28	2
B	7/151	11	2	22	2
	52/153	107	5	69	3
	170	34	2	32	2
	116/128	460	12	242	11
	180	75	3	66	3
	136	124	5	74	4
	38/206	5	1	31	2
	138	123	3	62	4
	98	2	1	5	1
	107	221	6	43	2
C	168	25	3	15	2
	237	48	3	14	3
	139/140	181	7	56	3
	141	47	2	21	2
	173	103	6	189	9
	142	12	1	21	2
	248	847	14	308	13
	174/247	696	16	331	14
	144/161/164	146	8	45	3
	163/235	33	2	6	2
D	108	104	4	65	3
	110	160	5	67	3
	118	46	3	28	2
	145	2	1	25	2
	179	28	2	20	2
	175	77	3	32	2
	157	2	1	9	1
	158	6	1	4	1
	159	3	1	1	1
	165	8	1	1	1
	253	153	5	82	5

Supplementary Table 10. Cercopithecoid skull and mandible fragments recovered from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

	NISP				Total
	Right	Left	R/L	Indet.	
Skull Fragments					64
Maxilla	7	2	/	/	9
Frontal	7	6	/	4	17
Parietal	6	4	/	10	20
Occipital	2	1	2	/	5
Temporal	4	3	/	6	13
Sphenoid	/	/	/	/	/
Incisive	/	/	/	/	/
Nasal	/	/	/	/	/
Lacrymal	/	/	/	/	/
Zygomatic	4	7	/	/	11
Palatine	/	/	/	/	/
Ethmoid	/	/	/	/	/
Mandible	6	4	1	0	11
Isolated Teeth	27	24	/	3	54
Mandible fragments with teeth	/	1	/	/	1
Maxilla fragments with teeth	/	/	/	/	/

Supplementary Table 11. Cercopithecoid dental elements recovered from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

	Teeth (isolated and maxillary/mandibular)			
	Upper		Lower	
	Right	Left	Right	Left
Unid	3			
dc	/	/	/	/
dp3	/	/	/	/
dp4	/	/	1	/
I1	2	3	1	1
I2	1	2	2	1
C	3	2	3	1
P3	/	1	2	/
P4	2	1	/	1
M1	2	3	/	2
M2	3	1	1	2
M3	2	2	2	1

Supplementary Table 12. Cercopithecoid pectoral and pelvic girdle elements and vertebrae recovered from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Patella		3	2	/	5
Scapula		7	4	4	15
Clavicle		2	1	/	3
Pelvis		7	10	/	17
	Ischium	9	8	/	
	Ilium	6	10	/	
	Acetabulum	4	3	/	
	Pubis	3	2	/	
Vertebrae					31
	Cervical		2		
	Thoracic		2		
	Lumbar		3		
	Sacral		0		
	Caudal		24		

Supplementary Table 13. Cercopithecoid hand and foot elements recovered from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Metacarpal	MC1	4	2	/	6
	MC2	4	3	/	7
	MC3	5	4	/	9
	MC4	3	3	/	6
	MC5	2	3	/	5
TOTAL					33
Carpal	Trapezium			/	
	Trapezoid	1	0	/	1
	Capitate	2	1	/	3
	Hamate	1	1	/	2
	Scaphoid	2	0	/	2
	Lunate	1	1	/	2
	Pyramidal	0	1	/	1
	Pisiform			/	
TOTAL					11
Metatarsal	MT1	4	3	/	7
	MT2	6	3	/	9
	MT3	5	4	/	9
	MT4	4	5	/	9
	MT5	4	1	/	5
TOTAL					39
Tarsals	Astragalus	1	1	/	2
	Calcaneus	1	3	/	4
	Cuboid	/	1	/	1
	Navicular	1	/	/	1
	Cuneiform	/	/	/	/
TOTAL					8
Metapodial Shaft Fragments					28
Phalanges					54

Supplementary Table 14. Primate long bone fragments recovered from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

	NISP									Total
	Proximal			Diaphyses			Distal			
	Right	Left	Indet	Right	Left	Indet	Right	Left	Indet	
Humerus	4	2	/	12	11	10	2	3	/	44
Ulna	4	1	/	5	6	2	1	1	/	20
Radius	2	1	/	7	4	5	1	2	/	22
Femur	4	2	/	31	20	16	4	5	/	82
Tibia	1	3	/	10	8	4	1	2	/	29
Fibula	1	/	/	7	8	2	/	1	/	19

Supplementary Table 15. Cercopithecoid skull and mandible fragments recovered from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

	NISP				Total
	Right	Left	R/L	Indet.	
Skull Fragments					10
Maxilla	/	2	/	/	2
Frontal	/	/	/	/	/
Parietal	1	/	/	3	4
Occipital	/	/	/	/	/
Temporal	1	/	/	1	2
Sphenoid	/	/	/	/	/
Incisive	/	/	/	/	/
Nasal	/	/	/	/	/
Lacrymal	/	/	/	/	/
Zygomatic	1	1	/	/	2
Palatine	/	/	/	/	/
Ethmoid	/	/	/	/	/
Mandible	3	3	/	/	6
Isolated Teeth	3	3	/	/	6
Mandible fragments with teeth	3	3	/	/	6
Maxilla fragments with teeth	/	1	/	/	1

Supplementary Table 16. Cercopithecoid dental elements recovered from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

Unid	Teeth (isolated and maxillary/mandibular)			
	Upper		Lower	
	Right	Left	Right	Left
	/			
dc	/	/	/	/
dp3	/	/	/	/
dp4	/	/	/	/
I1	/	/	1	/
I2	/	/	/	/
C	/	1	2	1
P3	/	/	/	/
P4	/	/	/	/
M1	/	1	/	/
M2	/	/	/	/
M3	/	/	/	/

Supplementary Table 17. Cercopithecoid pectoral and pelvic girdle elements and vertebrae recovered from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

		NISP		Total
		Right	Left	
Patella		/	1	1
Scapula		7	5	15
Clavicle		1	/	1
Pelvis				19
	Ischium	6	4	/
	Ilium	3	4	2
	Acetabulum	5	4	4
	Pubis	2	3	1
Vertebrae				18
	Cervical		3	
	Thoracic		2	
	Lumbar		2	
	Sacral		1	
	Caudal		10	

Supplementary Table 18. Cercopithecoid hand and foot elements recovered from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Metacarpal	MC1	/	/	/	/
	MC2	/	1	/	1
	MC3	2	1	/	3
	MC4	1	2	/	3
	MC5	1	/	/	1
TOTAL					8
Carpal	Trapezium	/	/	/	/
	Trapezoid	/	/	/	/
	Capitate	/	/	/	/
	Hamate	/	/	/	/
	Scaphoid	/	/	/	/
	Lunate	1	/	/	1
	Pyramidal	/	/	/	/
	Pisiform	/	/	/	/
TOTAL					1
Metatarsal	MT1	1	3	/	4
	MT2	3	/	/	3
	MT3	/	2	/	2
	MT4	1	/	/	1
	MT5	/	2	/	2
TOTAL					12
Tarsals	Astragalus	2	1	/	3
	Calcaneus	4	5	/	9
	Cuboid	1	/	/	1
	Navicular	/	/	/	/
	Cuneiform	/	/	/	/
TOTAL					26
Metapodial Shaft Fragments					6
Phalanges					4

Supplementary Table 19. Cercopithecoid long bone fragments recovered from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

	NISP									Total
	Proximal			Diaphyses			Distal			
	Right	Left	Indet	Right	Left	Indet	Right	Left	Indet	
Humerus	1	2	/	3	2	3	3	2	/	16
Ulna	18	13	/	10	12	/	1	2	/	56
Radius	2	1	/	2	3	6	4	3	1	22
Femur	2	4	/	6	4	13	3	2	/	34
Tibia	1	2	/	4	3	4	2	3	/	19
Fibula	2	1	/	6	4	2	3	1	/	19

Supplementary Table 20. Cercopithecoid skull and mandible fragments recovered from the Early Holocene layers (Phase B) of Fa-Hien Lena.

	NISP				Total
	Right	Left	R/L	Indet.	
Skull Fragments					109
Maxilla	6	7	8	/	21
Frontal	4	2	/	3	9
Parietal	8	7	/	32	47
Occipital	2	1	1	1	5
Temporal	5	8	/	15	28
Sphenoid	/	/	/	/	/
Incisive	/	1	/	/	1
Nasal	1	/	/	/	1
Lacrymal	/	/	/	/	/
Zygomatic	3	2	/	/	5
Palatine	/	/	/	/	/
Ethmoid	/	/	/	/	/
Mandible	2	6	2	1	11
Isolated Teeth	24	35	/	4	65
Mandible fragments with teeth	/	3	1	/	4
Maxilla fragments with teeth	1	3	/	/	4

Supplementary Table 21. Cercopithecoid dental elements recovered from the Early Holocene layers (Phase B) of Fa-Hien Lena.

Unid	Teeth (isolated and maxillary/mandibular)			
	Upper		Lower	
	Right	Left	Right	Left
	4			
dc	1	/	1	/
dp3	/	/	/	1
dp4	1	2	2	/
I1	1	/	1	/
I2	/	2	3	1
C	1	1	1	2
P3	1	2	1	3
P4	/	2	/	1
M1	4	7	2	2
M2	/	3	1	2
M3	1	1	4	3

Supplementary Table 22. Cercopithecoid pectoral and pelvic girdle elements and vertebrae recovered from the Early Holocene layers (Phase B) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Patella		2	1	/	3
Scapula		7	8	15	30
Clavicle		1	2	/	3
Pelvis					64
	Ischium	14	16	/	
	Ilium	31	28	2	
	Acetabulum	18	21	/	
	Pubis	26	21	/	
Vertebrae					79
	Cervical		6		
	Thoracic		5		
	Lumbar		9		
	Sacral		2		
	Caudal		57		

Supplementary Table 23. Cercopithecoid hand and foot elements recovered from the Early Holocene layers (Phase B) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Metacarpal	MC1	4	3	/	7
	MC2	8	8	/	16
	MC3	8	9	/	17
	MC4	3	5	/	8
	MC5	1	3	/	4
TOTAL					48
Carpal	Trapezium	/	/	/	/
	Trapezoid	/	1	/	1
	Capitate	2	/	/	2
	Hamate	2	/	/	2
	Scaphoid	1	1	/	2
	Lunate	/	1	/	1
	Pyramidal	/	1	/	1
	Pisiform	/	/	/	/
TOTAL					9
Metatarsal	MT1	3	4	/	7
	MT2	9	6	/	15
	MT3	10	7	/	17
	MT4	7	11	/	18
	MT5	3	2	/	5
TOTAL					62
Tarsals	Astragalus	4	5	/	9
	Calcaneus	5	5	/	10
	Cuboid	4	1	/	5
	Navicular	1	1	/	2
	Cuneiform	2	2	/	4
TOTAL					30
Metapodial Shaft Fragments					80
Phalanges					149

Supplementary Table 24. Cercopithecoid long bone fragments recovered from the Early Holocene layers (Phase B) of Fa-Hien Lena.

	NISP									Total
	Proximal			Diaphyses			Distal			
	Right	Left	Indet	Right	Left	Indet	Right	Left	Indet	
Humerus	4	3	/	15	13	28	6	8	/	77
Ulna	18	20	4	8	6	15	2	1	4	78
Radius	4	5	/	12	10	14	4	6	/	55
Femur	16	14	/	20	15	27	10	12	/	114
Tibia	4	5	/	18	16	6	4	2	/	55
Fibula	3	5	/	10	8	4	7	4	/	41

Supplementary Table 25. Cercopithecoid skull and mandible fragments recovered from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

	NISP				Total
	Right	Left	R/L	Indet.	
Skull Fragments					264
Maxilla	9	19	/	8	36
Frontal	11	11	1	11	34
Parietal	24	30	3	26	83
Occipital	5	5	8	4	22
Temporal	23	19	20	21	83
Sphenoid	/	/	/	/	/
Incisive	/	/	/	/	/
Nasal	2	0	0	0	2
Lacrymal	/	/	/	/	/
Zygomatic	5	8	/	/	13
Palatine	2	1	1	2	6
Ethmoid	/	/	/	/	/
Mandible	15	29	9	7	60
Isolated Teeth	114	112	/	18	244
Mandible fragments with teeth	1	4	/	/	5
Maxilla fragments with teeth	/	2	/	/	2

Supplementary Table 26. Cercopithecoid dental elements recovered from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

Unid	Teeth (isolated and maxillary/mandibular)			
	Upper		Lower	
	Right	Left	Right	Left
	18			
dc	2	/	1	1
dp3	1	2	1	/
dp4	4	2	2	1
I1	6	7	7	8
I2	7	4	4	6
C	8	10	8	7
P3	3	4	4	6
P4	7	3	3	1
M1	5	5	13	9
M2	3	5	11	14
M3	3	3	11	14

Supplementary Table 27. Cercopithecoid pectoral and pelvic girdle elements and vertebrae recovered from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

	NISP			Total
	Right	Left	Indet.	
Patella	6	4	/	10
Scapula	34	27	3	64
Clavicle	4	6	/	10
Pelvis	29	30	/	59
Ischium	14	7	/	
Ilium	20	21	/	
Acetabulum	12	16	/	
Pubis	8	12	/	
Vertebrae				238
Cervical		28		
Thoracic		36		
Lumbar		37		
Sacral		10		
Caudal		127		

Supplementary Table 28. Cercopithecoid hand and foot elements recovered from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

		NISP			Total
		Right	Left	Indet.	
Metacarpal	MC1	9	4	/	13
	MC2	17	12	/	29
	MC3	12	15	/	27
	MC4	6	5	/	11
	MC5	7	4	/	11
TOTAL					91
Carpal	Trapezium	1	/	/	1
	Trapezoid	/	1	/	1
	Capitate	2	2	/	4
	Hamate	/	1	/	1
	Scaphoid	/	2	/	2
	Lunate	1	/	/	1
	Pyramidal	1	1	/	2
	Pisiform	/	/	/	/
TOTAL					12
Metatarsal	MT1	5	6	/	11
	MT2	12	16	/	28
	MT3	17	13	/	30
	MT4	14	16	/	30
	MT5	7	9	/	16
TOTAL					115
Tarsals	Astragalus	17	11	/	28
	Calcaneus	18	21	/	39
	Cuboid	1	4	/	5
	Navicular	3	4	/	7
	Cuneiform	3	2	/	5
TOTAL					84
Metapodial Shaft Fragments					123
Phalanges					135

Supplementary Table 29. Cercopithecoid long bone fragments recovered from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

	NISP									Total
	Proximal			Diaphyses			Distal			
	Right	Left	Indet	Right	Left	Indet	Right	Left	Indet	
Humerus	14	10	2	20	19	47	21	16	5	154
Ulna	19	14	8	20	18	13	2	1	9	104
Radius	9	8	/	15	14	13	7	5	/	71
Femur	20	25	/	23	15	55	12	5	6	161
Tibia	14	12	/	15	8	22	4	2	/	77
Fibula	2	3	/	20	13	20	3	1	/	62

Supplementary Table 30. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the cercopithecoid remains recorded from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

		MNE	MAU	% MAU
Scapula		11	5.5	39.29
Clavicle		3	1.5	10.71
Humerus		10	5.5	39.29
Radius		8	4	28.57
Ulna		5	2.5	17.86
Metacarpal	1	6	3	21.43
	2	7	3.5	25
	3	9	4.5	32.14
	4	6	3	21.43
	5	5	2.5	17.86
Carpal	Trapezium	/	/	/
	Trapezoid	2	1	7.14
	Capitate	3	1.5	10.71
	Hamate	1	0.5	3.57
	Scaphoid	3	1.5	10.71
	Lunate	2	1	7.14
	Pyramidal	/	/	/
	Pisiform	/	/	/
Pelvis	Ilium	12	6	42.86
	Ischium	10	5	35.71
	Acetabulum	7	3.5	25
	Pubis	5	2.5	17.86
Femur		28	14	100
Patella		5	2.5	17.86
Tibia		12	6	42.86
Fibula		13	6.5	46.3
Metatarsal	1	7	3.5	25
	2	9	4.5	32.14
	3	9	4.5	32.14
	4	9	4.5	32.14
	5	5	2.5	17.86
Tarsal	Astragalus	2	1	7.14
	Calcaneus	4	2	14.29
	Cuboid	1	0.5	3.57
	Navicular	1	0.5	3.57
Phalanges	Proximal	31	1.55	11.07
	Intermediate	18	0.9	6.43

	Distal	5	0.25	1.79
Vertebra	Cervical	2	0.29	2.07
	Thoracic	2	0.17	1.21
	Lumbar	3	0.43	3.07
	Sacral	/	/	/
	Caudal	24	1.33	9.5
Mandible		7	3.5	25

Supplementary Table 31. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the cercopithecoid remains recorded from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

		MNE	MAU	% MAU
Scapula		36	18	80
Clavicle		10	5	22.22
Humerus		37	18.5	82.22
Radius		17	8.5	37.78
Ulna		33	16.5	73.33
Metacarpal	1	13	6.5	28.89
	2	29	14.5	64.44
	3	27	13.5	60
	4	11	5.5	24.44
	5	11	5.5	24.44
Carpal	Trapezium	1	0.5	2.22
	Trapezoid	1	0.5	2.22
	Capitate	4	2	8.89
	Hamate	1	0.5	2.22
	Scaphoid	2	1	4.44
	Lunate	1	0.5	2.22
	Pyramidal	2	1	4.44
	Pisiform	/	/	/
Pelvis	Ilium	31	15.5	68.89
	Ischium	21	10.5	46.67
	Acetabulum	28	14	62.22
	Pubis	20	10	44.44
Femur		45	22.5	100
Patella		10	5	22.22
Tibia		26	13	57.78
Fibula		32	16	71.11
Metatarsal	1	11	5.5	24.44
	2	29	14.5	64.44
	3	30	15	66.67
	4	30	15	66.67
	5	16	8	35.56
Tarsal	Astragalus	28	14	62.22
	Calcaneus	39	19.5	86.67
	Cuboid	5	2.5	11.11
	Navicular	7	3.5	15.56

Phalanges	Proximal	78	3.9	17.33
	Intermediate	42	2.1	9.33
	Distal	15	0.75	3.33
Vertebra	Cervical	28	4	17.78
	Thoracic	36	3	13.33
	Lumbar	37	5.29	23.51
	Sacral	10	10	44.44
	Caudal	127	7.05	31.36
Mandible		34	17	75.56

Supplementary Table 32. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the cercopithecoid remains recorded from the Early Holocene layers (Phase B) of Fa-Hien Lena.

		MNE	MAU	% MAU
Scapula		15	7.5	39.47
Clavicle		3	1.5	7.89
Humerus		14	7	36.84
Radius		10	5	26.32
Ulna		38	19	100
Metacarpal	1	7	3.5	18.42
	2	16	8	42.11
	3	17	8.5	44.74
	4	8	4	21.05
	5	4	2	10.53
Carpal	Trapezium	/	/	/
	Trapezoid	1	0.5	2.63
	Capitate	2	1	5.26
	Hamate	2	1	5.26
	Scaphoid	2	1	5.26
	Lunate	1	0.5	2.63
	Pyramidal	1	0.5	2.63
	Pisiform	/	/	/
Pelvis	Ilium	28	14	73.68
	Ischium	20	10	52.63
	Acetabulum	36	18	94.74
	Pubis	26	13	68.42
Femur		30	15	78.95
Patella		3	1.5	7.89
Tibia		9	4.5	23.68
Fibula		11	5.5	28.95
Metatarsal	1	7	3.5	18.42
	2	15	7.5	39.47
	3	17	8.5	44.74
	4	18	9	47.37
	5	5	2.5	13.16
Tarsal	Astragalus	9	4.5	23.68
	Calcaneus	10	5	26.32
	Cuboid	5	2.5	13.16
	Navicular	2	1	5.26
Phalanges	Proximal	89	4.45	23.42

	Intermediate	42	2.1	11.05
	Distal	18	0.9	4.74
Vertebra	Cervical	6	0.86	4.53
	Thoracic	5	0.42	2.21
	Lumbar	9	1.29	6.79
	Sacral	2	2	10.53
	Caudal	57	3.17	16.68
Mandible		12	6	31.58

Supplementary Table 33. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the cercopithecoid remains recorded from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

		MNE	MAU	% MAU
Scapula		12	6	38.71
Clavicle		1	0.5	3.23
Humerus		5	2.5	16.13
Radius		7	3.5	22.58
Ulna		31	15.5	100
Metacarpal	1	/	/	/
	2	1	0.5	3.23
	3	3	1.5	9.68
	4	3	1.5	9.68
	5	1	0.5	3.23
Carpal	Trapezium	/	/	/
	Trapezoid	/	/	/
	Capitate	/	/	/
	Hamate	/	/	/
	Scaphoid	/	/	/
	Lunate	1	0.5	3.23
	Pyramidal	/	/	/
	Pisiform	/	/	/
Pelvis	Ilium	7	3.5	22.58
	Ischium	10	5	32.26
	Acetabulum	9	4.5	29.03
	Pubis	5	2.5	16.13
Femur		6	3	19.35
Patella		1	0.5	3.23
Tibia		5	2.5	16.13
Fibula		4	2	12.9
Metatarsal	1	4	2	12.9
	2	3	1.5	9.68
	3	2	1	6.45
	4	1	0.5	3.23
	5	2	1	6.45
Tarsal	Astragalus	3	1.5	9.68
	Calcaneus	9	4.5	29.03
	Cuboid	1	0.5	3.23
	Navicular	/	/	/
Phalanges	Proximal	2	0.1	0.65
	Intermediate	2	0.1	0.65

	Distal	/	/	/
Vertebra	Cervical	3	0.43	2.77
	Thoracic	2	0.17	1.1
	Lumbar	2	0.29	1.87
	Sacral	1	1	6.45
	Caudal	10	0.56	3.61
Mandible		6	3	19.35

Supplementary Table 34. Cercopithecoid long bone fragmentation (NISP:MNE) and fragment completeness.

Phase	Element	NISP:MNE Ratio	Circumferential completeness			Length completeness		
			100%	> 50%, <100%	<50%	100%	> 50%, <100%	<50%
Phase A	Humerus	3.2	37.5	37.5	25	0	6.25	93.75
	Ulna	1.81	67.86	25	7.14	0	26.79	73.21
	Radius	3.14	77.27	9.09	13.64	0	50	50
	Femur	5.67	76.47	14.71	8.82	0	14.71	85.29
	Tibia	3.8	78.95	10.53	10.53	0	26.32	73.68
	Fibula	4.75	57.89	42.11	0	5.26	26.32	68.42
Phase B	Humerus	5.5	24.68	28.57	46.75	0	18.18	81.82
	Ulna	2.05	71.79	20.51	7.69	0	24.36	75.64
	Radius	5.5	61.82	29.09	9.09	0	18.18	81.82
	Femur	3.8	8.77	25.44	65.79	0	29.82	70.18
	Tibia	6.11	36.36	25.45	38.18	0	36.36	63.64
	Fibula	3.73	75.61	24.39	0	2.44	26.83	70.73
Phase C	Humerus	4.16	62.99	10.39	26.62	0	26.62	73.38
	Ulna	3.15	69.23	20.19	10.58	0	50.96	49.04
	Radius	4.18	45.07	38.03	16.9	0	25.35	74.65
	Femur	3.58	22.98	25.47	51.55	0	19.88	80.12
	Tibia	2.96	38.96	35.06	25.97	0	38.96	61.04
	Fibula	1.94	72.58	24.19	3.23	0	19.48	75.81
Phase D	Humerus	4.4	9.09	15.91	75	0	36.36	63.64
	Ulna	4	60	30	10	0	25	75
	Radius	2.75	59.09	22.73	18.18	0	18.18	81.82
	Femur	2.93	4.88	8.54	86.59	0	24.39	75.61
	Tibia	2.42	6.9	27.59	65.52	0	13.79	86.21
	Fibula	1.46	57.89	36.84	5.26	0	47.37	52.63

Supplementary Table 35. Anthropic modifications in bone fragments recovered from Fa-Hien Lena.

Phase	Context	TNF	NISP	Burning				Butchery	Tools/Ornaments
				Partial	Total	PC	TC		
A	216	661	362	3	29	22	25	9	4
	131	114	53	6	7	22	7	2	2
	135	181	74	1	3	2	1	2	10
B	7/151	62	39	3	7	15	9	0	2
	52/153	451	331	24	12	48	32	1	1
	170	188	84	16	23	15	14	3	10
	116/128	2281	838	45	133	39	20	2	18
	180	380	165	22	15	26	23	1	5
	136	535	256	32	70	85	23	6	7
	38/206	193	66	2	12	23	24	1	3
	138	210	161	3	11	3	5	1	4
	98	35	13	1	2	3	1	0	0
	107	260	260	3	4	1	1	0	1
C	168	87	42	4	13	11	6	3	2
	237	93	71	3	5	2	3	1	4
	139/140	576	257	29	59	25	7	14	9
	141	94	78	3	5	2	1	0	5
	173	605	293	105	185	78	121	1	3
	142	207	41	1	2	0	0	1	2
	248	2354	1512	84	147	39	28	24	59
	174/247	2294	1161	66	113	73	67	11	53
	144/161/164	245	196	8	13	2	1	0	3
	163/235	60	60	3	4	1	1	0	4
D	108	318	237	0	17	19	2	1	1
	110	414	267	12	15	17	7	0	2
	118	238	86	13	41	34	14	2	1
	145	36	29	0	1	0	1	1	1
	179	132	90	2	2	19	28	1	1
	175	288	143	12	36	19	10	1	15
	157	55	26	3	6	7	4	0	2
	158	64	34	0	5	1	1	0	1
	159	31	12	2	2	0	1	0	1
	165	38	12	0	4	1	1	0	1
	253	705	280	29	71	62	33	3	10

Supplementary Table 36. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the sciurid remains recorded from the mid-Holocene layers (Phase A) of Fa-Hien Lena.

		NISP			MNE	MAU	% MAU
		Right	Left	Indet			
Scapula		/	1	/	1	0.5	20
Humerus	Proximal	1	/	/	3	1.5	60
	Shaft	2	1	/			
	Distal	/	2	/			
Radius	Proximal	1	/	/	3	1.5	60
	Shaft	1	2	/			
	Distal	/	/	/			
Ulna	Proximal	3	2	/	5	2.5	100
	Shaft	1	1	/			
	Distal	/	/	/			
Metacarpal	1	/	/	/	/	/	/
	2	1	/	/	1	0.5	20
	3	/	1	/	1	0.5	20
	4	1	/	/	1	0.5	20
	5	/	/	/	/	/	/
Carpal	Trapezium	/	/	/	/	/	/
	Trapezoid	/	/	/	/	/	/
	Capitate	/	/	/	/	/	/
	Hamate	/	/	/	/	/	/
	Scaphoid	/	/	/	/	/	/
	Lunate	/	/	/	/	/	/
	Pyramidal	/	/	/	/	/	/
	Pisiform	/	/	/	/	/	/
Pelvis	Ilium	2	1	/	3	1.5	60
	Ischium	1	3	/			
	Acetabulum	1	3	/			
	Pubis	1	1	/			
Femur	Proximal	2	1	/	3	1.5	60
	Shaft	1	1	/			
	Distal	1	1	/			
Tibia	Proximal	2	/	/	2	1	40
	Shaft	1	1	/			
	Distal	/	1	/			
Metatarsal	1	/	/	/	/	/	/
	2	/	/	/	/	/	/
	3	1	/	/	1	0.5	20
	4	/	1	/	1	0.5	20
	5	/	/	/	/	/	/
Tarsal	Astragalus	1	/	/	1	0.5	20
	Calcaneus	/	1	/	1	0.5	20
Phalanges	Proximal	1			1	0.05	2
	Intermediate	2			2	0.1	4
	Distal	/			/	/	/
Vertebra	Cervical	/			/	/	/

Thoracic		1		/	0.08	3.2
Lumbar		/		/	/	/
Sacral		/		/	/	/
Caudal		4		/	0.13	5.2
Mandible	1	2	/	3	1.5	60

Supplementary Table 37. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the sciurid remains recorded from the Early Holocene layers (Phase B) of Fa-Hien Lena.

		NISP			MNE	MAU	% MAU
		Right	Left	Indet			
Scapula		3	4	/	7	3.5	16.3
Humerus	Proximal	19	23	/	42	21	97.7
	Shaft	24	23	/			
	Distal	14	18	/			
Radius	Proximal	16	15	/	31	15.5	72.1
	Shaft	12	10	/			
	Distal	1	2	/			
Ulna	Proximal	21	22	/	43	21.5	100
	Shaft	26	26	/			
	Distal	1	2	/			
Metacarpal	1	/	/	/	/	/	/
	2	1	2	/	3	1.5	7
	3	2	1	/	3	1.5	7
	4	1	/	/	1	0.5	2.3
	5	/	/	/	/	/	/
Carpal	Trapezium	1	/	/	1	0.5	2.3
	Trapezoid	/	/	/	/	/	/
	Capitate	/	/	/	/	/	/
	Hamate	/	/	/	/	/	/
	Scaphoid	/	1	/	1	0.5	2.3
	Lunate	/	/	/	/	/	/
	Pyramidal	/	/	/	/	/	/
	Pisiform	/	/	/	/	/	/
Pelvis	Ilium	11	12	/	31	15.5	72.1
	Ischium	18	14	/			
	Acetabulum	21	19	/			
	Pubis	14	17	/			
Femur	Proximal	21	22	/	43	21.5	100
	Shaft	19	21	/			
	Distal	4	5	/			
Patella		1	/	/	1	0.5	2.3
Tibia	Proximal	14	16	/	30	15	69.8
	Shaft	15	11	/			
	Distal	4	6	/			
Metatarsal	1	/	/	/	/	/	/
	2	1	3	/	4	2	9.3
	3	1	2	/	3	1.5	7
	4	2	2	/	4	2	9.3
	5	1	/	/	4	2	9.3
Tarsal	Astragalus	1	1	/	2	1	4.7
	Calcaneus	12	8	/	20	10	46.5
Phalanges	Proximal	24			24	1.2	5.6
	Intermediate	28			28	1.4	6.5
	Distal	2			2	0.1	0.5

Vertebra	Cervical	7	7	1	4.7
	Thoracic	14	4	0.93	4.3
	Lumbar	11	11	1.83	8.5
	Sacral	2	2	2	9.3
	Caudal	34	34	1.13	5.3
Mandible		4 3 /	7	3.5	16.3

Supplementary Table 38. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the sciurid remains recorded from the Terminal Pleistocene layers (Phase C) of Fa-Hien Lena.

		NISP			MNE	MAU	% MAU
		Right	Left	Indet			
Scapula		14	16	/	30	15	51.7
Humerus	Proximal	8	7	/	51	25.5	87.9
	Shaft	24	36	10			
	Distal	11	8	/			
Radius	Proximal	4	1	/	21	10.5	36.2
	Shaft	8	16	8			
	Distal	3	4	/			
Ulna	Proximal	18	24	/	42	21	72.4
	Shaft	28	21	/			
	Distal	1	1	/			
Metacarpal	1	1	2	/	3	1.5	5.2
	2	4	2	/	6	3	10.3
	3	3	4	/	7	3.5	12.1
	4	2	4	/	6	3	10.3
	5	1	1	/	2	1	3.5
Carpal	Trapezium	1	/	/	1	0.5	1.7
	Trapezoid	/	/	/	/	/	/
	Capitate	1	1	/	2	1	3.5
	Hamate	1	/	/	1	0.5	1.7
	Scaphoid	/	/	/	/	/	/
	Lunate	/	1	/	1	0.5	1.7
	Pyramidal	1	/	/	1	0.5	1.7
	Pisiform	/	/	/	/	/	/
Pelvis	Ilium	24	21	/	41	20.5	70.7
	Ischium	14	11	/			
	Acetabulum	28	34	/			
	Pubis	8	11	/			
Femur	Proximal	17	22	/	58	29	100
	Shaft	44	35	28			
	Distal	22	21	/			
Patella		1	2	/	3	1.5	5.2
Tibia	Proximal	14	11	/	37	18.5	63.8
	Shaft	21	19	7			
	Distal	13	17	/			
Metatarsal	1	1	1	/	2	1	3.5
	2	1	2	/	3	1.5	5.2
	3	8	6	/	14	7	24.1
	4	7	4	/	11	5.5	18.9
	5	2	1	/	3	1.5	5.2
Tarsal	Astragalus	3	4	/	7	4.5	15.5
	Calcaneus	18	21	/	39	19.5	67.2
Phalanges	Proximal	48			48	2.4	8.3
	Intermediate	52			52	2.6	9
	Distal	14			14	0.7	2.4

Vertebra	Cervical	14	14	2	6.9
	Thoracic	8	8	0.6	2.1
	Lumbar	7	7	1.2	4.1
	Sacral	5	4	4	13.8
	Caudal	87	87	2.9	10
Mandible		21 31 /	48	24	82.8

Supplementary Table 39. Minimum Number of Element (MNE) and percent Minimum Animal Unit (%MAU) values for the sciurid remains recorded from the Late Pleistocene layers (Phase D) of Fa-Hien Lena.

		NISP			MNE	MAU	% MAU
		Right	Left	Indet			
Scapula		2	4	/	6	3	15
Humerus	Proximal	4	4	/	12	6	30
	Shaft	7	8	/			
	Distal	2	5	/			
Radius	Proximal	2	1	/	9	4.5	22.5
	Shaft	9	4	/			
	Distal	1	1	/			
Ulna	Proximal	10	8	/	18	9	45
	Shaft	9	12	/			
	Distal	/	/	2			
Metacarpal	1	1	/	/	1	0.5	2.5
	2	/	2	/	2	1	5
	3	1	2	/	3	1.5	7.5
	4	1	1	/	2	1	5
	5	1	/	/	1	0.5	2.5
Carpal	Trapezium	/	/	/	/	/	/
	Trapezoid	/	/	/	/	/	/
	Capitate	/	/	/	/	/	/
	Hamate	/	/	/	/	/	/
	Scaphoid	/	/	/	/	/	/
	Lunate	/	/	/	/	/	/
	Pyramidal	/	/	/	/	/	/
	Pisiform	/	/	/	/	/	/
Pelvis	Ilium	8	7	/	11	5.5	27.5
	Ischium	4	4	/			/
	Acetabulum	7	4	/			/
	Pubis	3	4	/			/
Femur	Proximal	4	8	/	40	20	100
	Shaft	24	20	/			
	Distal	8	7	/			
Patella		1	1	/	2	1	5
Tibia	Proximal	4	5	/	17	8.5	42.5
	Shaft	8	10	/			
	Distal	8	6	/			
Metatarsal	1	/	/	/	/	/	/
	2	1	/	/	1	0.5	2.5
	3	/	1	/	1	0.5	2.5

		4	2	1	/	3	1.5	7.5
		5	/	/	/	/	/	/
Tarsal	Astragalus		1	3	/	4	2	10
	Calcaneus		3	3	/	6	3	15
Phalanges	Proximal			12		12	0.6	3
	Intermediate			18		18	0.9	4.5
	Distal			4		4	0.2	1
Vertebra	Cervical			8		8	1.14	20
	Thoracic			6		6	0.46	15
	Lumbar			4		4	0.67	10
	Sacral			2		2	2	10
	Caudal			28		28	0.93	4.7
Mandible			6	4	/	10	5	25

Supplementary Table 40. Results of Kruskal-Wallis test and post-hoc pairwise comparison of mammalian taxa grouped by body size in different occupational phases the site considering the NISP²⁹.

Kruskal-Wallis Test H= 1.543, p= 0.6705, no significance between sample medians		
	Mann-Whitney Test with Bonferroni sequential correction for p	Dunn's Test with Bonferroni sequential correction for p
Phase A vs. B	0.5993	0.5201
Phase A vs. C	0.2984	0.2177
Phase A vs. D	0.6733	0.6296
Phase B vs. C	0.6004	0.5555
Phase B vs. D	0.9166	0.8723
Phase C vs. D	0.5309	0.4531

Supplementary Table 41. Results of Kruskal-Wallis test and post-hoc pairwise comparison of mammalian taxa grouped by body size in different occupational phases the site considering the MNI²⁹.

Kruskal-Wallis Test H= 1.324, p= 0.7235, no significance between sample medians		
	Mann-Whitney Test with Bonferroni sequential correction for p	Dunn's Test with Bonferroni sequential correction for p
Phase A vs. B	0.4005	0.402
Phase A vs. C	0.4005	0.2818
Phase A vs. D	0.7518	0.6473
Phase B vs. C	0.7518	0.8086
Phase B vs. D	0.7533	0.7064
Phase C vs. D	0.6742	0.536

Supplementary Table 42. Result of t test and descriptive statistics for the difference in burning in Cercopithecoid and Sciurid specimens across different layers²⁹.

No. of burnt/calced specimens	Cercopithecoids			Sciurids			95% CI for Mean difference	t	df
	M	SD	n	M	SD	n			
	19.882	19.392	34	19.471	18.094	34			
							-8.6694, 9.493	0.0905	66

Appendix 3. Lithic Materials from Fa Hien Lena

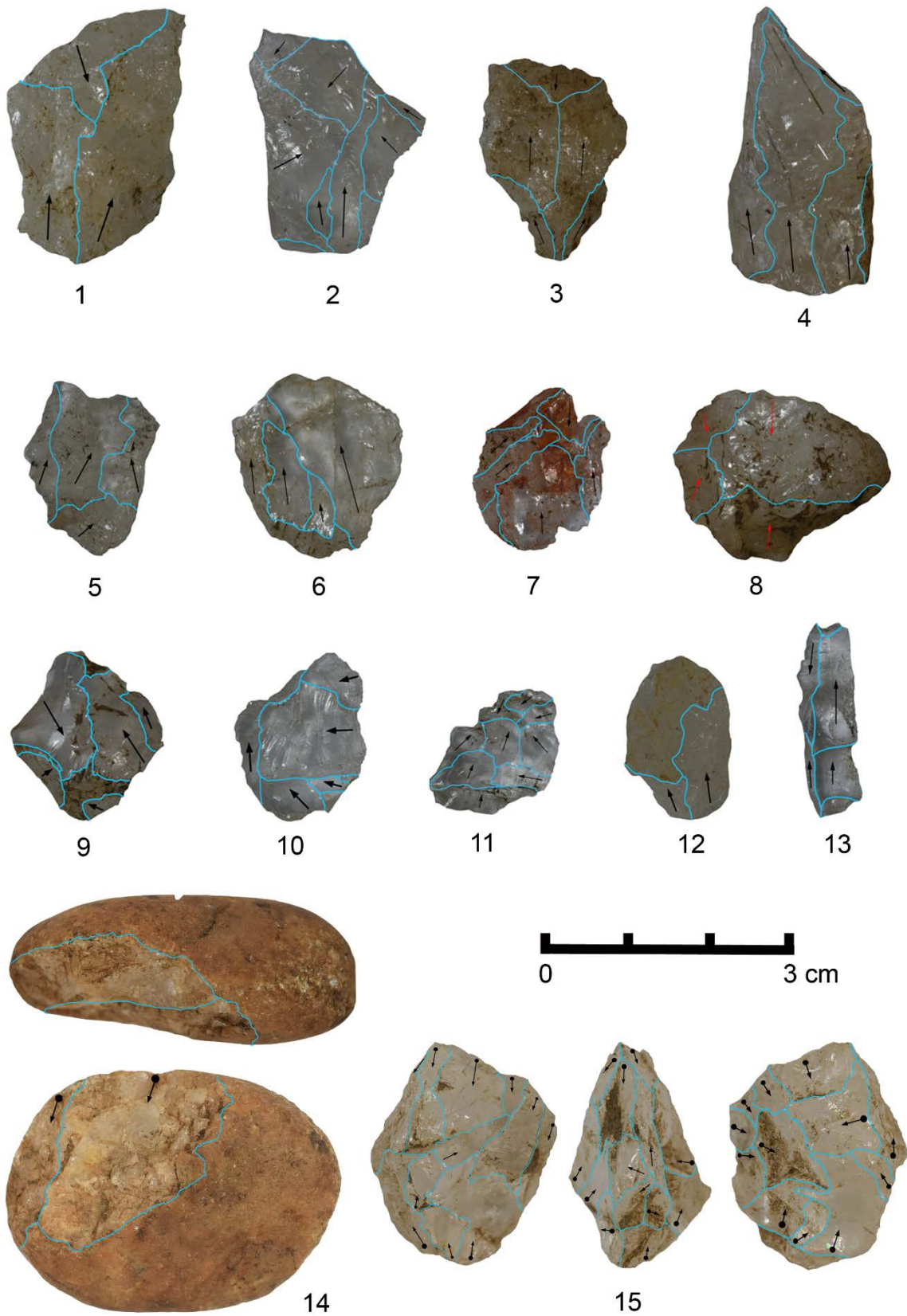
The use of bipolar technology was identified through diacritic reading of scar patterns on flakes and cores. This method involves holding the core on an anvil and striking it with a hard hammer. During the knapping process, force is transmitted on the vertical or tangential axis of the core and flakes are produced by the contact with the stone hammer and the anvil³⁰. This results in the recurrent presence of bidirectional scars on both cores and flake dorsal surfaces, alongside crushing of elements in contact with either the hammer or anvil. (Supplementary Figure 17). At Fa-Hien Lena, the bipolar method was used consistently throughout the excavated assemblages. Generally, quartz nodules were struck along the longest axis in order to maximize the size of the byproducts. However, in some examples, the prehistoric knappers changed the striking platform during reduction rotating the core by 90 degrees and exploiting the smaller surface. This technical expedient permits a better exploitation of irregular pebbles and produces flakes with orthogonal scars on the dorsal surface (Supplementary Figure 17 n° 9, 10, 11). At the site, the aim of the knapping activities is the production of small flakes and the presence of small blades and bladelets could be considered as an unintentional outcome rather than a planned strategy. In fact, in the lithic collection, laminar cores and byproducts for maintaining the convexities in the laminar reduction are absent.

The flake assemblage is mainly composed of fragments and little chips, whereas complete blanks are less numerous (Supplementary Table 43-44). This is very common in contexts of quartz bipolar reduction due to the simple organization of the core and the absence of predetermination on the byproducts. Furthermore, bipolar technology typically involves more limited control on the use of force in contrast to other technologies, with a bending stress applied resulting in cracking of the platform, creation of large numbers of small chips, or fracturing flakes along the percussion axis (siret). Phase D exhibits the highest proportion of siret (longitudinal fractures) fragments (14.5%), followed by Phase B (13.7%), Phase A (12.6%) and Phase C (10.2%). Analysis of the complete flakes indicates their varying occurrence throughout the excavated sequence, with higher frequencies recorded in Phase D (Supplementary Table 43-44). Except for some outliers, the comparison between the median values of the length of unbroken artefacts shows minimal differences between the phases of occupation (Supplementary Figure 18).

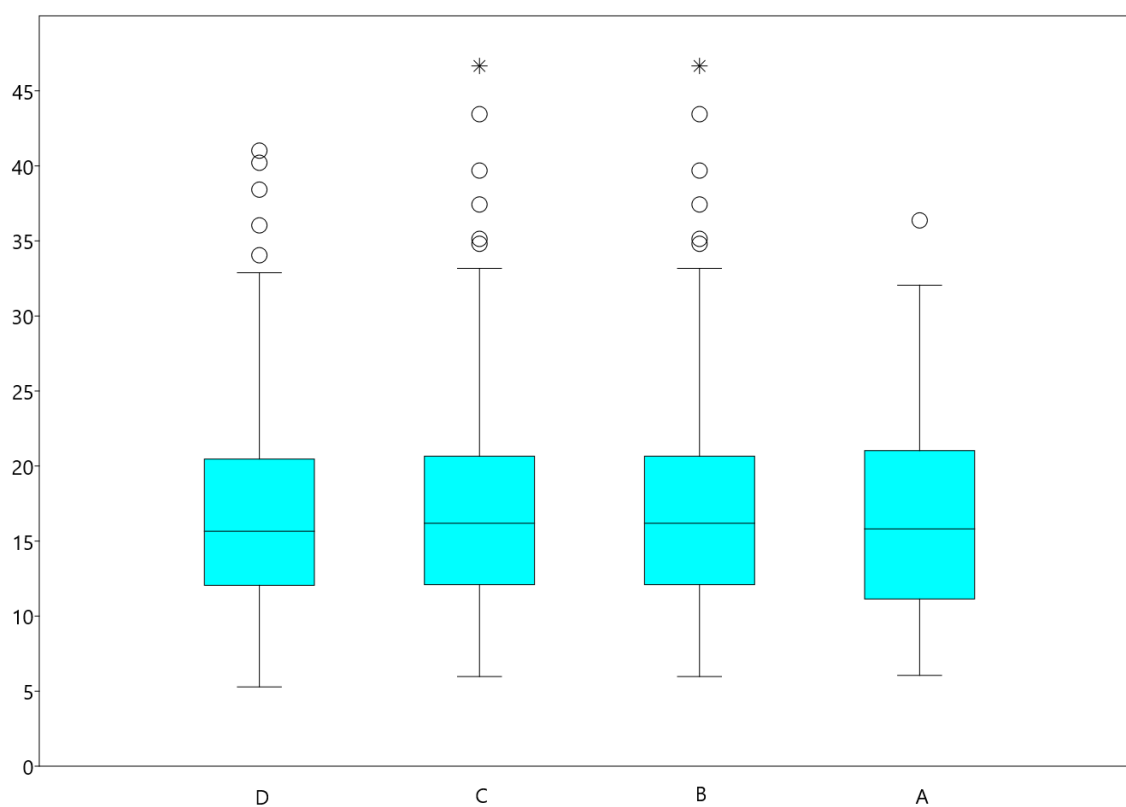
Retouched tools occur in extremely low frequency, numbering only three microliths discovered in Phase D (Supplementary Table 43-44). The microlith is a small stone tool made on a bladelet or a small flake, characterized by a steep and blunting retouch along one edge³¹. The microlith could be laminar, if the blank has an elongated shape, or geometric, if the retouch changes the morphology of the blank in trapezoidal, triangular or crescent shape. Ethnographic data on modern-hunter gatherers and experimental studies indicate that microliths are commonly used hafted in composite tools or projectiles, and employed as hunting weapons³²⁻³⁴.

A crescent microlith with a continuous backed retouch along one side and two notch fractures on the cutting edge was recorded in context 165 (Supplementary Figure 19A). A backed retouch on both edges were documented, respectively, in context 158 on a laminar microlith fragment with a bend fracture, and in context 175 on a laminar microlith with a step terminating breakage (Supplementary Figure 19B-C). Patterns of breakage on the three microliths are currently under study, but are likely to have originated from impacts occurring during hunting activities.

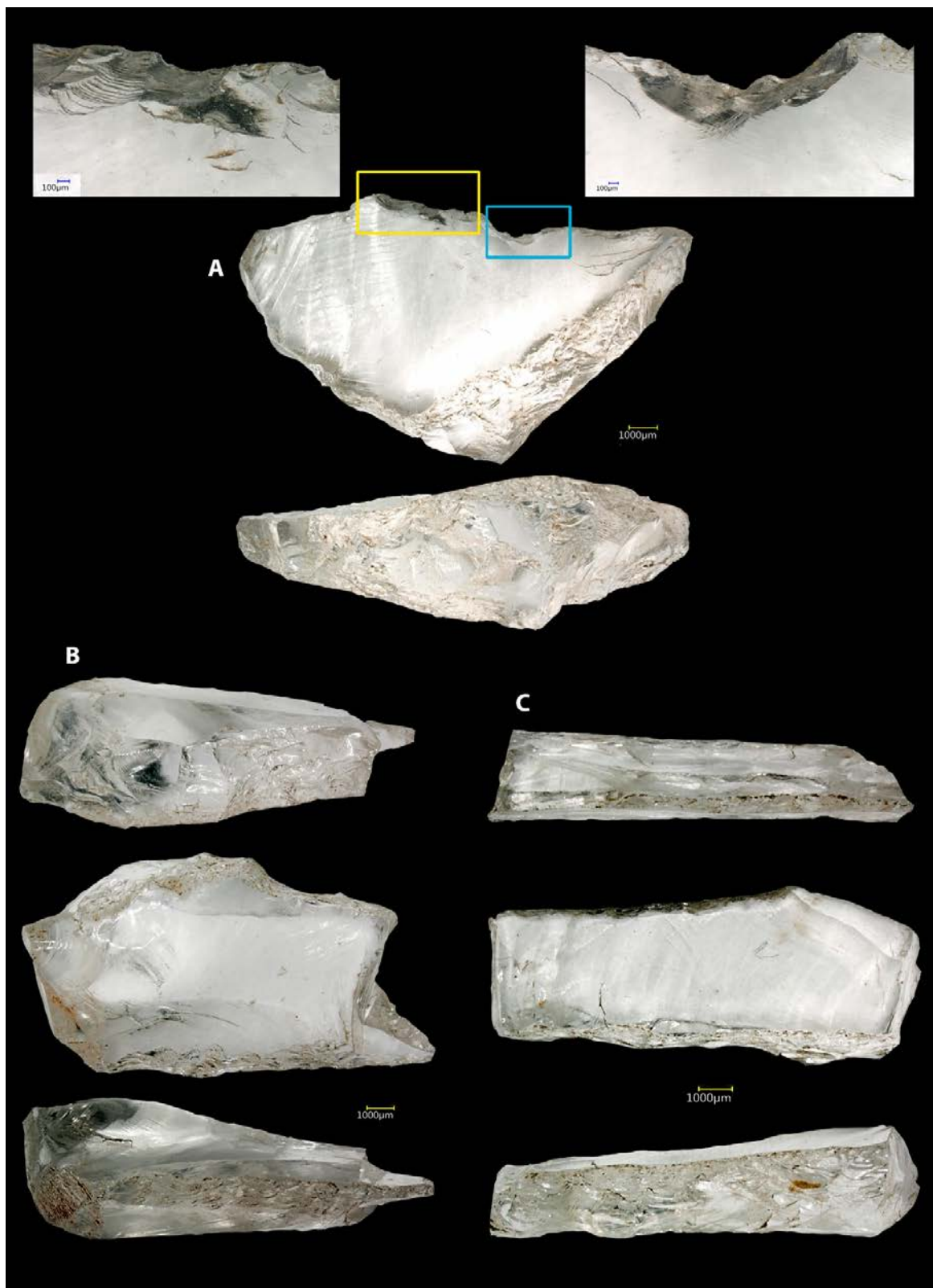
The analysis of the lithic materials from Fa-Hien Lena indicates a continuity in the use of bipolar knapping on anvil from the Late Pleistocene to the late Holocene. This method is very flexible and allows a greater exploitation of the nodule, in comparison with other technologies, producing relatively large blanks from small cores³⁴. Moreover, the simple operative scheme enables the knapper to produce small blanks that are mostly straight and lacking pronounced bulbs on the ventral surfaces. These features make the bipolar flakes/blades particularly appropriate to be hafted after a minimal reshaping of the cutting edges. Similar technological strategies to those identified at Fa-Hien Lena have also been documented at Batadomba Lena and Kitulgala Beli-Lena, supporting the widespread diffusion of this complex behavior in the wet zone of Sri Lanka^{36,37}.



Supplementary Figure 17. Bipolar flakes from Phase D (1, 2, 4, 6, 10, 11), Phase C (3, 7, 9, 13), Phase B (5, 12) and bipolar cores from Phase D (15) and Phase C (14).



Supplementary Figure 18. Comparison of the length of complete flakes and blades in the different phases of occupation of Fa-Hien Lena Cave.



Supplementary Figure 19. Microlithic tools of Phase D context 165 (A), context 158 (B) and context 175 (C).

Supplementary Table 43. Total amount by contexts of the lithic materials of Fa-Hien Lena Cave.

	Layer	Flake	Blade	Fragments	Debris	Tools	Core	Core Frag.	Hammer	Total
A	216	8		14	19		1	2		44
	131	71	5	200	299		7	6		588
	31=32=135	19		61	28		3	1		112
B	7 = 151	11		25	14			2		52
	52=153	6		19	43		1	1		70
	170	7		7	5		2	2		23
	116=128	71	4	287	254		8	4		628
	136	42	1	73	71			1		188
	38=206	15		31	31					77
	138	10		27	52		3			92
	98	1		3	1					5
	107				7					7
C	168	9		23	67					99
	237	10		47	84		3	1		145
	139=140	30	1	140	361		4	4	1	541
	141	12		81	207		2		1	303
	173	7		26	46					79
	142	14		14	89		1			118
	248	6	3	13	6				1	29
	174 =247	75	1	212	352		7	5		652
	144=161=164	23	1	45	104			1		174
	163=235	5		9	32					46
D	108	10		31	38			1		80
	110	3		8			2			13
	118	11	3	33	5					52
	145	33	3	83	99		3			221
	179	20		15	43					78
	175	16	1	49	77	1		2	4	150
	157	11		10	17					38
	158	28	1	33	2	1	1	3		69
	159	28	3	86	3			3		123
	165	19	2	26	1	1				49

	253	25	1	65	32		2			125
Total		656	30	1796	2489	3	50	39	7	5070

Supplementary Table 44. Total amount of lithic materials in the different occupational phases of Fa-Hien Lena Cave.

Phase	Flake	Blade	Fragments	Debris	Tools	Core	Core Frag.	Hammer	Total
A	98	5	275	346		11	9		744
%	<i>13.2</i>	<i>0.7</i>	<i>37</i>	<i>46.5</i>		<i>1.5</i>	<i>1.2</i>		<i>100</i>
B	163	5	472	478		14	10		1142
%	<i>14.3</i>	<i>0.4</i>	<i>41.3</i>	<i>41.9</i>		<i>1.2</i>	<i>0.9</i>		<i>100</i>
C	191	6	610	1348		17	11	3	2186
%	<i>8.7</i>	<i>0.3</i>	<i>27.9</i>	<i>61.7</i>		<i>0.8</i>	<i>0.5</i>	<i>0.1</i>	<i>100</i>
D	204	14	439	317	3	8	9	4	998
%	<i>20.4</i>	<i>1.4</i>	<i>44</i>	<i>31.8</i>	<i>0.3</i>	<i>0.8</i>	<i>0.9</i>	<i>0.4</i>	<i>100</i>
Total	656	30	1796	2489	3	50	39	7	5070
%	<i>12.9</i>	<i>0.6</i>	<i>35.4</i>	<i>49.1</i>	<i>0.1</i>	<i>1</i>	<i>0.8</i>	<i>0.1</i>	<i>100</i>

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Summary

Sri Lanka is becoming increasingly renowned in the international literature as a region of great importance for studying Late Pleistocene dispersals of *Homo sapiens* across Asia and, more specifically, the early adaptation of human populations to tropical rainforest environments in this part of the world. By the late 1980s and early 1990s Sri Lanka had already provided evidence for the earliest human skeletal material and microlithic artefacts anywhere in South Asia. During the last two decades this research was followed up by problem orientated research, however multidisciplinary analysis of early human sites in Sri Lanka, including the application of robust chronological techniques and systematic analyses of lithic and osseous technologies, have remained limited. This thesis presents datasets obtained from new excavation, zooarchaeological, archaeobotanical, lithic, bone tool, and symbolic material culture analyses at two cave sites in the tropical rainforest zone of Sri Lanka, Fa-Hien Lena and Beli-lena Kitulgala. In doing so, it provides the earliest dates for definitive human occupation of the island *c.* 48-45,000 years ago, and detailed insights into the resources used by members of our species as they rapidly colonized the southern tip of South Asia.

The first excavation was performed at the site of Fa-Hien Lena, a major Late Pleistocene cave deposit in Sri Lanka located in southwest of the island. My application of novel methodological and multidisciplinary approaches to the site, greatly improved our knowledge of this already-important sequence of tropical human occupation. In particular, state-of-the-art Acid Base Oxidation pretreatment of charcoal samples prior to dating have pushed back the known date of occupation of the rainforests of Sri Lanka 10-7,000 years earlier than expected, and in line with evidence in Borneo and New Guinea. The first paper in this thesis focused not just on these new dates but also detailed taxonomic and taphonomic analysis of the faunal assemblage recovered.

This revealed the specialized, sophisticated hunting of semi-arboreal and arboreal monkey and squirrel populations from ca. 48,000 - 45,000 years ago, in a tropical rainforest environment. I argue that these data highlight that the early capture of small, elusive mammals was part of the adaptive flexibility of *Homo sapiens* that allowed it to rapidly colonize a series of extreme environments including the lowland rainforests of Sri Lanka – environments that have no evidence of earlier occupation by other hominin species.

Previous studies that have focused on the emergence of human procurement of small, difficult-to-catch animals, or a ‘broad spectrum’ approach to hunting and gathering, had been associated with climate change or demographic pressures beginning c. 20,000 years ago. Nevertheless, these studies were primarily based in Europe and the Levant. The data we uncovered from Sri Lanka demonstrates that this adaptive strategy was, in fact, an accompaniment of the earliest human populations colonizing tropical rainforest environments in South Asia, rather than a later shift due to external stimuli. In this paper, I have also demonstrated that the fauna at Fa Hien cave were hunted by employing complex projectile technology which involved the use of bone tools as projectile points. The high degree of fragmentation of small mammal bones, particularly those of monkeys, in addition to the presence of half finished (blanks) and finished tools suggest that Fa Hien Cave was a workshop for tool manufacture. Among the finished tools recovered were bone points with clear evidence of high-velocity impact fracture, suggesting they were most likely used to hunt the arboreal animals, perhaps as part of a composite projectile (blow dart or arrow).

The second paper in this thesis focused on the enigmatic microlithic assemblages of the Sri Lankan Wet Zone rainforest. Our analyses demonstrated that Fa-Hien Lena represents the earliest microlith assemblage in South Asia (c. 48,000–45,000 cal. years BP). Moreover, our data highlight that the lithic technology of Fa-Hien Lena did not change significantly over the long span of human occupation, indicating a successful, stable technological adaptation to the rainforest ecology.

Therefore, alongside the bone tool technologies mentioned above, I argue that microlith assemblages were an important part of the adaptive flexibility that enabled *Homo sapiens* to colonize a diversity of ecological settings during his expansion within and beyond Africa. Microliths are often interpreted to be part of composite tools, including projectile weapons, and efficient hunting strategies by modern humans. However, previously, they have often been linked to the exploitation of medium-large bodied prey in open grassland or ‘savannah’ settings.

Finally, the third paper in this thesis draws on a second series of excavations at the site of Kitulgala Beli-lena. As at Fa-Hien Lena, renewed chronometric study of charcoal at Kitulgala Beli-lena produced much older dates for human occupation, in this case 45,000-44,000 years ago, making this site roughly contemporaneous to Fa-Hien Lena and the slightly later sequence of Batadombalena. This paper also presents analysis of excavated lithic materials from Kitulgala Belilena Cave, numbering some 15,000 artefacts. Similar to Fa-Hien lena, this research identified the entire production trajectories by using detailed technological attribute analysis and making use of all the products and by-products of lithic manufacture. The goal of these analyses was to understand the chronological and technological patterns and changes during the Late Pleistocene to early Holocene at Fa-Hien lena and Kitulgala Beli-lena caves. Moreover, comparison of Kitulgala Beli-lena with Fa-Hien lena has enabled us to begin to talk about human use of rainforest ‘landscapes’ rather than isolated sites.

To conclude the thesis I compare the novel data produced from Fa-Hien Lena and Kitulgala Belilena with the existing archaeological datasets from the Sri Lankan Wet Zone rainforest and beyond. Moreover, I place this data in its South Asian and broader Asian context. Sri Lanka is increasingly making major contributions to our understandings of the technological, cultural, and ecological capacities of our species more widely. It is becoming increasingly apparent that what defines our species, in contrast to other hominins, is its capacity to adapt to the whole diversity of environments

that our planet has to offer. The colonization of deserts, high altitude environments, the palaeoarctic, and, in Sri Lanka, tropical rainforests began in earnest from the Late Pleistocene. Microlith and organic technologies, rather than being associated with coastal or ‘savannah’ resource use, were in fact part of a flexible package that enabled *Homo sapiens* to rapidly adapt to these diverse ecological situations. The work of this thesis, and the future work it will hopefully stimulate, is driving some of these shifting perceptions, and will hopefully do so for many years to come.

Zusammenfassung

Sri Lanka gewinnt in der internationalen Literatur immer mehr an Bedeutung für die Erforschung der Verbreitung des *Homo sapiens* in Asien im Spätpleistozän und insbesondere für die frühe Anpassung der menschlichen Bevölkerung an die tropischen Regenwaldumgebungen in diesem Teil der Welt. Bereits Ende der 1980er und Anfang der 1990er Jahre wurden in Sri Lanka die frühesten menschlichen Skelettmaterialien und mikrolithischen Artefakte in ganz Südasien nachgewiesen. In den letzten zwei Jahrzehnten wurde diese Forschung durch problemorientierte Forschung ergänzt, wobei die multidisziplinäre Analyse früher menschlicher Lebensräume in Sri Lanka, einschließlich der Anwendung robuster chronologischer Techniken und systematischer Analysen lithischer und Knochen basierter Technologien, begrenzt geblieben ist. Diese Doktorarbeit stellt Datensätze aus neuen Ausgrabungen, zooarchäologischen, archäobotanischen, lithischen, Knochenwerkzeuganalysen und symbolischen Materialkulturanalysen an zwei Höhlenstandorten, Fa-Hien Lena und Beli-lena Kitulgala, in der tropischen Regenwald-Zone von Sri Lanka vor. Damit liefert diese Arbeit die frühesten Daten für die endgültige menschliche Okkupation der Insel vor etwa 48-45.000 Jahren und detaillierte Einblicke in die Ressourcen, die von Mitgliedern unserer Spezies genutzt wurden, die die Südspitze Südasiens schnell kolonisierten. Die erste Ausgrabung erfolgte an der Stelle von Fa-Hien Lena, einer bedeutenden spätpleistozänen Höhle in Sri Lanka im Südwesten der Insel. Die Anwendung neuartiger methodischer und multidisziplinärer Ansätze auf diesen Standort hat unser Wissen über den Hergang der menschlichen Besiedlung in den Tropen erheblich verbessert. Insbesondere aufgrund der hochmodernen Vorbehandlung von Holzkohleproben für die Radiokohlenstoff Datierung war es möglich den Zeitraum der Besiedlung der Regenwälder Sri Lankas um 10-7.000 Jahre früher als erwartet präzise zu datieren. Die Daten zeigen eine Übereinstimmung mit den Befunden in Borneo und Neuguinea. Die erste Publikation in dieser Arbeit fokussiert auf diese neuen Daten, sowie auch

auf die detaillierte taxonomische und taphonomische Analyse der faunalen Assemblage. Diese offenbart die spezialisierte, anspruchsvolle Jagd auf halb- und baumartige Affen- und Eichhörnchenpopulationen vor ca. 48.000 - 45.000 Jahren in einer tropischen Regenwaldumgebung. Unsere Daten zeigen, dass die frühe Jagd kleiner, schwer fassbarer Säugetiere Teil der adaptiven Flexibilität des Homo sapiens war, die es ihm ermöglichte, eine Reihe von extremen Umgebungen schnell zu kolonisieren, einschließlich der Tieflandregenwälder Sri Lankas - Umgebungen, die keinen Beweis für eine frühere Besiedlung durch andere Homininarten haben.

In früheren Studien, die sich auf die Entwicklung der menschlichen Jagd von kleinen, schwer zu fangenden Tieren oder einen Ansatz des "breiten Spektrums" bei der Jagd und Sammlung konzentriert haben, wurde mit Klimawandel oder dem demografischen Druck seit etwa 20.000 Jahren argumentiert. Diese Studien fokussierten hauptsächlich auf Europa und dem Levante. Die von uns aus Sri Lanka gewonnenen Daten zeigen, dass diese Anpassungsstrategie tatsächlich eine Begleiterscheinung der frühesten menschlichen Populationen war, die tropische Regenwaldgebiete in Südasien besiedelten, und nicht eine spätere Verschiebung aufgrund externer Reize. Zudem zeigen die Überreste gefundener Fauna in der Höhle Fa Hien, dass sie mit Hilfe komplexer Projektiltechnik gejagt wurden, bei der Knochenwerkzeuge als Projektilspitzen Verwendung fanden. Der hohe Fragmentierungsgrad der kleinen Säugetierknochen, insbesondere der Affenknochen, sowie das Vorhandensein von halbfertigen (Rohlinge) und fertigen Werkzeugen deuten darauf hin, dass die Fa-Hien-Höhle für die Werkzeugherstellung genutzt wurde. Zu den fertigen Werkzeugen gehörten Knochenspitzen mit deutlichen Hinweisen auf Hochgeschwindigkeitsfrakturen. Damit ist anzunehmen, dass sie höchstwahrscheinlich zur Jagd auf Baumtiere verwendet wurden, vermutlich als Teil eines Verbundgeschosses (Blaspfeil oder Pfeil).

Die zweite Publikation in dieser Arbeit konzentriert sich auf die rätselhaften mikrolithischen Assemblagen des Regenwaldes der sri-lankischen Nass Zone. Unsere Analysen haben ergeben, dass Fa-Hien Lena die früheste Mikrolith-Assemblage in Südasien darstellt (ca. 48.000-45.000 cal. Jahre BP). Darüber hinaus zeigen unsere Daten, dass sich die Lithische-Technologie von Fa-Hien Lena über lange Zeit der menschlichen Tätigkeit nicht wesentlich verändert hat, was auf eine erfolgreiche und stabile technologische Anpassung an die Ökologie des Regenwaldes hindeutet. Daher kann argumentiert werden, dass neben den oben genannten Knochenwerkzeugtechnologien die Mikrolith-Assemblagen ein wichtiger Teil der adaptiven Flexibilität waren, die es dem Homo sapiens ermöglichte, während seiner Expansion innerhalb und außerhalb Afrikas eine Vielzahl von ökologischen Umgebungen zu kolonisieren. Mikrolithen werden oft als Teil von Verbundwerkzeugen, einschließlich Projektilwaffen, und effizienten Jagdstrategien des modernen Menschen interpretiert. Zuvor wurden sie jedoch oft mit der Jagd auf mittelgroßer Beute in offenem Grünland oder in Savannengebieten in Verbindung gebracht.

Die dritte Publikation in dieser Arbeit basiert auf der erneuten Ausgrabung von Kitulgala Beli-lena. Wie bei Fa-Hien Lena führte die verbesserte chronometrische Untersuchung der Holzkohle in Kitulgala Beli-lena zu viel älteren Daten für die menschliche Besiedlung. In diesem Fall auf 45.000-44.000 Jahren, was die Nutzung dieses Ortes etwa zeitgleich mit Fa-Hien Lena und der etwas späteren Sequenz von Batadomba-lena macht. Diese Publikation stellt auch die Analyse von ausgegrabenen lithischen Materialien aus der Höhle Kitulgala Belilena mit rund 15.000 Artefakten vor. Ähnlich wie bei Fa-Hien lena konnte die gesamte Produktionskette identifiziert werden, indem detaillierte technologische Attributanalysen unter Verwendung aller Produkte und Nebenprodukte der lithischen Herstellung durchgeführt wurden. Ziel dieser Analysen war es, die chronologischen und technologischen Muster und Veränderungen vom Spätpleistozän zum frühen Holozän bei Fa-Hien lena und Kitulgala Beli-lena Höhlen zu verstehen. Darüber hinaus hat der Vergleich von

Kitulgala Beli-lena mit Fa-Hien lena es ermöglicht, über die menschliche Nutzung von Regenwaldlandschaften und nicht über isolierte Standorte zu sprechen.

Abschließend wurden in dieser Doktorarbeit die neu gewonnenen Daten von Fa-Hien Lena und Kitulgala Beli-lena mit den vorhandenen archäologischen Datensätzen aus dem Regenwald der Sri Lankischen Nasszone und darüber hinaus verglichen. Anschließend wurden diese Daten in den südasiatischen und breiteren asiatischen Kontext gestellt.

Sri Lanka leistet zunehmend einen wichtigen Beitrag zu unserem Verständnis der technologischen, kulturellen und ökologischen Fähigkeiten unserer Spezies im weiteren Sinne. Es wird immer deutlicher, dass das, was unsere Spezies im Gegensatz zu anderen Homininen ausmacht, ihre Fähigkeit ist, sich an die ganze Vielfalt der Umwelt anzupassen, die unser Planet zu bieten hat. Die Kolonisation von Wüsten, hochgelegenen Gebieten, der Paläoarktis und, wie in Sri Lanka, der tropischen Regenwälder begann bereits im Spätpleistozän. Mikrolith und organische Technologien waren in der Tat Teil eines flexiblen Pakets, das es dem Homo sapiens ermöglichte, sich schnell an diese unterschiedlichen ökologischen Gegebenheiten anzupassen, anstatt auf die Nutzung von Küsten- oder Savannenressourcen angewiesen zu sein. Die Forschung dieser Doktorarbeit wird hoffentlich zukünftige Arbeit anregen und die veränderte Wahrnehmung vorantreiben.

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Excavation research Prehistoric cave in “Rajagala”
- 2017
Excavation research Prehistoric cave in “Kitulgala Beli lena cave”
- 2017
Paleo Lakes sampling project in Sri Lanka

- 2019 Excavation research Prehistoric cave in “Bundala”
- 2019 Botanical reference sampling in Sri Lanka

An International Archaeological Experience

- 2012 Scientific methods of stone tools Analysis- University of Oxford, United Kingdom
- 2012 Field survey, Excavation methods and Laboratory skills University of Oxford, United Kingdom

Excavations done during Post Graduate Studies

- 2010 Excavation research “Girawar ” conducted by Deccan Collage (India)
- 2010 Excavation research “Nasik ” conducted by Deccan Collage (India)
- 2011 Excavation research “Farmana Harappa Site” by Deccan College (India)
- 2011 Excavation research “Raki gadi” conducted by Deccan College (India)
- 2013 Excavation research “Jubbha Valley” (Saudi Arabia) by University of Oxford
- 2013 Excavation research “Dhman ” (Saudi Arabia) by University of Oxford
- 2014 Excavation research “ Dawadme ” (Saudi Arabia) by University of Oxford
- 2016 Excavation research Prehistoric cave in “Rajagala”
- 2017 Excavation research Prehistoric cave in “Kitulgala Beli lena cave”
- 2017 Paleo Lakes sampling project in Sri Lanka

Conference and seminars

- 2004 Conference on heritage Conservation in south and south east Asia, Titled Heritage Conservation : New Alliance for past, present, and future organized by World Monuments Fund and International Council on Monuments and Sites (ICOMOS) Sri Lanka held in Colombo Sri Lanka - 28-31 August 2004
- 2010 A participant as a Secretariat of the conference on Society of South Asian Archaeology (SOSAR) held in Colombo Sri Lanka - 2010.
- 2011 A participant as a Secretariat of the conference on International Association for Asian Heritage (IAAH) held in Colombo Sri Lanka - 2011.
- 2018 A participant as a scientist UISPP Conference “ Earliest evidence for tropical rainforest exploitation in South Asia” Paris - 2018

Professional Affiliations

- I. Member of the Sri Lanka Council of Archaeologists – 2011 to date
- II. Member of the Society of South Asian Archaeology (SOSAR) (International) – 2009 to date

III. Member of the International Association for Asian Heritage (IAAH) – 2011 to date

04/12/2019

.....
Date


.....
Oshan Wedage Manjula Chanaka

Piliyandala (Colombo),
04.12.2019

To the Dean
of the Faculty of Philosophy
Fürstengraben 1
07743 Jena, Germany

Based on the attached scientific treatise (dissertation):

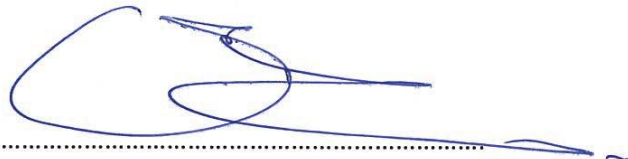
**New investigations into the Late Pleistocene and Early Holocene rainforest
prehistory of Sri Lanka**

I request the opening of the doctoral procedure for the award of the academic
degree:

- ☐ Dr. phil.
- ☐ PhD

I have agreed amicably with the supervisor on the following examination form
according to § 11, paragraph 1 PromO of the Faculty of Philosophy:

- ☐ Disputation
- ☐ Colloquium

A handwritten signature in blue ink, consisting of a large, stylized 'C' followed by a series of loops and a long horizontal stroke.

Signature of the doctoral candidate

Piliyandala (Colombo),

04.12.2019

An den Dekan
der Philosophischen Fakultät
Fürstengraben 1
07743 Jena

Aufgrund der beigefügten wissenschaftlichen Abhandlung (Dissertation):

**New investigations into the Late Pleistocene and Early Holocene rainforest
prehistory of Sri Lanka**

bitte ich um Eröffnung des Promotionsverfahrens zur Verleihung des akademischen
Grades:

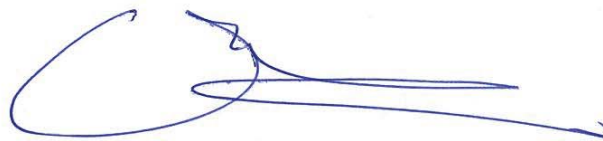
☐ Dr. phil.

☐ PhD X

Ich habe einvernehmlich mit dem/der Betreuer/in die folgende Prüfungsform lt. § 11,
Absatz 1 PromO der Philosophischen Fakultät vereinbart:

☐ Disputation (open)

☐ Kolloquium (small)



.....
Unterschrift des Doktoranden

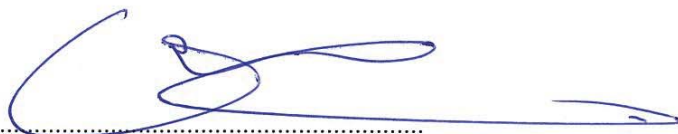
Declaration of honour

Hereby I declare

- (a) that I am aware of the applicable doctoral regulations,
- (b) that I have written the doctoral thesis myself and that I have not taken any text sections from another author or from my own examination papers without indicating them and that I have indicated all tools and sources used by myself in this work,
- (c) that I have mentioned all persons who have supported me in the selection and evaluation of the material as well as in the production of the manuscript,
- (d) that I have not used the assistance of a doctoral advisor and that third parties have neither directly nor indirectly received monetary benefits from me for work that is related to the content of the submitted doctoral thesis,
- (e) that I have not yet submitted this doctoral thesis as an examination paper for an academic examination,
- (f) that I have submitted neither the same thesis nor an essentially similar thesis, nor a different thesis as a doctoral thesis at another university.

OR

(f') that I have submitted another thesis with the title... (.....)at(....) university with the following result:(....)



Wedage Manjula Chanaka Oshan

04.12.2019